POTATO PEST MANAGEMENT IN CANADA

LUTTE CONTRE LES PARASITES DE LA POMME DE TERRE AU CANADA

EDITED BY:
G. BOITEAU / R.P. SINGH / R.H. PARRY

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Proceedings of a Symposium on Improving Potato Pest Protection held in Fredericton, New Brunswick, 27-29 January 1987, under the Canada-New Brunswick Agri-Food Development Agreement.

Comptes-rendus d'un Symposium sur L'Amelioration de la Lutte contre les Parasites de la Pomme de Terre tenu a Fredericton, Nouveau-Brunswick, 27-29 janvier 1987, avec le support de l'Entente Canada-Nouveau-Brunswick sur le Developpement du Secteur Agro-Alimentaire.

PREFACE

Potato production in Canada covers more than 110,000 ha and represents a value of more than 275 million dollars. It is an important crop. Without protection, some 62-85% of the yield could be lost to insects, weeds, pathogens and nematodes. With the controls presently applied, it is estimated that less than 6% of the yield is lost.

However, this apparently successful protection system is marred by problems: some actual, some upcoming. The management of most potato pests relies heavily on the use of chemical pesticides: insecticides, fungicides, herbicides and nematicides. At a time when only a few embryonic IPM programs are under way, some pest populations are becoming resistant to chemicals: the Colorado potato beetle to insecticides and the late blight to fungicides. The incidence of many pests, such as luteoviruses in the Western part of the country and mosaic viruses in the East, has been drastically reduced but they do persist as significant problems.

It is factors like those that stimulated us to hold a Symposium on Improving Potato Pest Protection in Fredericton, New Brunswick, on January 27-29, 1987. The objectives were to bring scientists together to discuss all aspects of potato pest management in Canada, to compile an inventory of Canadian problems and their solutions as they apply to different geographic areas, and to foster the cooperative approach to problem solving in an age of reduced resources. Twenty-seven specialists representing 7 of the 10 Canadian provinces were invited to prepare and present up-to-date reviews covering the different aspects of potato pest protection. More than 60 additional specialists attended the Symposium and shared their views with the speakers. The Symposium was followed by a Strategic Planning IPM Workshop on Potatoes organized by Agriculture Canada. The Report from the Workshop is available from Research Program Service, Research Branch, Agriculture Canada, Ottawa.

We thank the contributors for their cooperation and patience in the preparation of these Proceedings. Special thanks to Mr. Guy Bernard, of the New Brunswick Department of Agriculture, whose interest in the project helped make the publication of these Proceedings possible. We are very grateful to the Canada-New Brunswick Agri-Food Development Agreement who funded the Symposium and the printing of these Proceedings.

Organizing Committee

G. Boiteau
R.P. Singh
R.H. Parry

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REMARKS

by

THE HONORABLE HAZEN MYERS

New Brunswick Minister of Agriculture

It is my pleasure to welcome you to this busy two and a half day program on potatoes, here in Fredericton, the capital city of New Brunswick.

The potato industry is a very important part of the agricultural economy of this Province. Twenty-three percent of farm cash receipts in 1984 came from potatoes. This industry, like many others, must constantly adjust its production technology to meet changing consumer needs and a changing national and international economy.

The management of insects, viruses, bacteria, fungi, weeds and other pests that affect potato production has been very successful in this country. Every dollar invested in pest control has been returned many times over. However, the costs of controls are increasing steadily, and faster than the yields. It is good to recognize the progress accomplished and we should all be proud of it, but the challenge continues.

Looking at the program, I was pleased to see entomologists, plant pathologists, weed scientists, and crop protection managers meeting together across the barriers of disciplines. I have been given to understand that this is the first meeting of this kind in a long time to be held in Canada. I can assure you that your choice of the Maritimes has historical precedents. For example, the first agricultural society organized in Canada was the Society for Promoting Agriculture, in Nova Scotia in 1789. Prince Edward Island farmers established an Agricultural Society in 1827 for importing superior lines of livestock, and The New Brunswick Society for the Encouragement of Agriculture, Home Manufacturers, and Commerce, was established in 1850, long before any federal or provincial government departments for agriculture were established.

The theme of this Symposium is protection of potatoes from pests. This is very appropriate. The year 1987 is in fact the 75th anniversary of the establishment of the very discipline of protection in New Brunswick. In 1912, the Division of Entomology of Dominion of Canada, established a small entomological laboratory on the University of New Brunswick campus. Its main objective was the study of local insect problems, with an emphasis on natural control. The scope of investigations widened to encompass biological and taxonomic studies, insecticides, their effects on crops and product quality, and their use in pest-control programs.

Only three years later, in 1915, the Division of Botany opened a plant pathology laboratory in Fredericton. Running out or degeneration disease of potatoes in the Maritime Provinces in 1914 was the first virus disease of plants to be identified in Canada.

Concurrent to the fledging development of the discipline of plant protection in the federal laboratory, a New Brunswick Department of Agriculture was also being established. It resulted in co-operative work that benfitted the potato industry.

It has been noted in one of our departmental books "Humble Beginnings" that "if there was one major influence on the development of the modern potato industry in New Brunswick, it had to be the late G.C. Cunningham. He was a pathologist at the Federal Department of Agriculture Laboratory from 1914-1923. He encouraged growers to organize their seed production".

In the years since, there have been many others and the co-operation continues between federal and provincial establishments. The Organizing Committee of this Symposium, with its provincial and federal counterparts and its funding under the Federal-Provincial Agricultural Agreements are themselves good examples.

Welcome again to New Brunswick, and I wish you well in your scientific deliberations.

Thank you.

APHID AND VIRUS MANAGEMENT IN POTATOES IN EASTERN CANADA

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ABSTRACT

The potato industry in eastern Canada includes an important seed production component which accounts for over 90% of the total national production of seed potatoes. In order to satisfy the demands of its customers for high quality virus-free tubers, this seed industry requires programs for managing aphids and the plant viruses they transmit. The major aphid-borne viruses of concern are potato leafroll virus (PLRV) and the mosaic-causing potato virus Y (PVY). Of the four species of aphids which infest potatoes in the east, the green peach aphid is the main target of monitoring and control programs because of its superior efficiency as a vector.

A summary of aphid monitoring programs and typical control methods employed in the eastern provinces is presented. The field monitoring and aerial monitoring components of the New Brunswick "Aphid Alert Program" are described and the use of the data to create information and recommendations for potato growers and the potato industry is discussed. Recent developments in the New Brunswick program include the evaluation of a large suction trap for monitoring flights of aphids and the testing of techniques for simulating or forecasting the timing of critical accumulations of winged green peach aphids. Also outlined are some areas in aphid and virus management which require further knowledge and development in order to strengthen existing programs and to increase their impact.

RESUME

La production de pommes de terre de semence est une composante importante de l'industrie de la pomme de terre dans l'Est du Canada. Elle représente au-dessus de 90% de la production nationale totale en pommes de terre de semence. Pour satisfaire les besoins de ses clients, cette industrie a besoin de programmes spéciaux pour la gérance des pucerons et des virus des plantes qu'ils transmettent. Les principaux virus transmis par les pucerons son ceux de l'enroulement (PLRV) et de la mosaique (PVY). Bien qu'il y ait quatre espèces de pucerons susceptibles d'infester les plants de pommes de terre dans l'Est, le puceron vert du pêcher reçoit le plus d'attention dans les programmes d'inventaire et de contrôle à cause de sa très grande efficacité comme vecteur.

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Un résumé des principaux programmes d'inventaire des pucerons et des méthodes de lutte employées par les provinces de l'Est est présenté. Les composantes "végétale" et "aérienne" du programme "Alerte au Pucerons" au Nouveau-Brunswick sont décrites. La transformation des données en information et en recommendations pour les producteurs et l'industrie est ensuite discutée. L'évaluation d'un piège à succion de 12,2 m pour suivre les vols des pucerons et la mise au point de techniques de simulation ou de prévision du moment ou les populations de pucerons vert du pêcher dépassent les seuils critiques sont des développements récents du programme au Nouveau-Brunswick. Finalement, un bref aperçu des aspects concernant la gérance des pucerons et des virus des plantes qui requièrent le plus d'attention en recherche et en développement si l'on veut renforcer les programmes existants et augmenter leur impact est présenté en conclusion.

INTRODUCTION

The potato industries of the eastern provinces of Ontario, Quebec, New Brunswick, Prince Edward Island and Nova Scotia together produce around 75% of Canada's total production (Table I). With a production base of between 700 and 1000 acres, the small commercial potato industry of Newfoundland accounts for only 0.2% of the national total. The Atlantic provinces together produce almost 50% of the total national production.

Table I - 1986 Potato Production in Canada*

Province	Acreage	Ave. Yield (cwt.)	Production (000 cwt.)	% of Total
P.E.I.	70,000	255	17,850	29
N.B.	50,800	220	11,176	18
Que.	48,900	189	9,259	15
Man.	41,000	190	7,790	12
Ont.	32,200	229	7,356	12
Alta.	22,500	240	5,400	9
B.C.	8,000	260	2,080	3
N.S.	3,900	210	819	1
Sask.	2,550	190	484	1
Total	279,850	222	62,214	100

*Statistics Canada, November 14, 1986.

When we look at the production of seed potatoes, we find that the major potato-producing provinces of Prince Edward Island and New Brunswick grew around 87% of the seed produced in Canada in 1984 (Table II). In that same year, 77% of the total potato acreage of P.E.I. passed

Table II - Estimated Production of Seed Potatoes, 1984 Crop (in cwt.)*

Province	Production	% of Total
P.E.I.	9,374,863	64.4
N.B.	3,313,468	22.8
Alta.	549,611	3.8
Que.	500,730	3.4
Man.	418,727	2.9
B.C.	218,031	1.5
Ont.	87,308	0.6
Sask.	57,947	0.4
N.S.	32,956	0.2
Nfld.	6,384	-
Total	14,560,025	100.0

*Extracted from Potato Market Review 1984-85, Market Information Service, Agriculture Canada.

Table III - Disposition of Potatoes in P.E.I. and N.B., 5 Year Average 1980-85*

	% of Marketable Stock			
		P.E.I.		N.B.
Table		55.7		21.1
Seed - domestic -	3.8		4.3	
export -	13.1		9.7	
total -		16.9		14.1
Local Use & Processing		16.4		55.2
Seed for Next Crop		11.0		9.6
Total		100.0		100.0

*Extracted from Potato Market Review 1984-85, Market Information Service, Agriculture Canada.

inspection for seed, while 36% of the total N.B. acreage was certified (1). Table III indicates the disposition or actual end uses of the P.E.I. and N.B. potato crops averaged over a five year period, 1980-85. It can be seen that, although some certified seed potatoes may have ended up on the tablestock market or in processing plants, seed in both provinces comprised about one-quarter (28% in P.E.I. and 24% in N.B.) of the total potato crop. Also significant is the 13% of the P.E.I. potato crop and almost 10% of the N.B. crop which was exported as seed to the United States and offshore markets.

Quality standards for seed potatoes are quite stringent and export markets in particular demand tubers of the highest quality and as free from disease as possible. Since aphids (Homoptera: Aphididae) are considered the major vectors of several virus diseases in potatoes (see Singh & Boiteau and Stace-Smith, these proceedings), the control or management of these pests is particularly important in seed production areas. In fact, the "Aphid Alert" programs of New Brunswick and the State of Maine were implemented in response to a major problem with potato leaf roll virus (PLRV) in the early 1970's (8,15). The leafroll problem was especially apparent in the then expanding acreage of the susceptible variety, Russet Burbank. In this major french-fry variety, infection with leafroll not only reduces seed quality but can also affect processing and table quality through the development of tuber net necrosis (10).

In Atlantic Canada, aphids that infest potatoes have been regarded primarily as virus vectors since it is generally agreed that their populations rarely reach the level where they have a significant effect on yields (3).

THE APHIDS AND THEIR IMPORTANCE

Four species of aphids colonize potatoes in eastern Canada: the common potato aphid, Macrosiphum euphorbiae (Thomas), the buckthorn aphid, Aphis nasturtii Kaltenbach, the green peach aphid, Myzus persicae (Sulzer), and occasionally the foxglove aphid, Aulacorthum solani (Kaltenbach) (7).

Common Potato Aphid

This species overwinters as nymph-producing females in greenhouses and other sheltered places and as eggs on woody shrubs of the Rosaceae, e.g. rose (Rosa nitida Willd., R palustris Marsh. and R. rugosa Thunb.) and raspberry (Rubus idaeus L.). In New Brunswick, female nymphs hatch from the eggs in late April or early May (2,13) and feed on young leaves. Usually there are two or three generations of females produced on the overwintering host, during which time winged (alate) viviparous females mature and fly to various weeds and potato plants (13). This aphid is usually the first to appear on potatoes in the summer and can be found in most fields. Numbers build up and winged forms are produced. These can fly to other fields and infest them. Populations generally decline by early or mid-August and winged forms move back to their overwintering hosts. The common potato aphid is an inefficient vector of PLRV and potato virus Y (PVY)(14,15) (see also Singh & Boiteau, these proceedings).

Buckthorn Aphid

This aphid spends the winter as eggs on buckthorn (Rhamnus alnifolia L'Her., R. cathartica L. and R. frangula L.). Winged females start flying from buckthorn in early June. They first colonize weeds such as lady's-thumb (Polygonum persicaria L.), hemp-nettle (Galeopsis tetrahit L.) and shepherd's purse (Capsella bursa-pastoris (L.) Medic.) and then, by mid-July, the lower leaves of potatoes. Summer populations are generally localized, infesting only a small number of potato fields, however, this aphid is sometimes the most abundant species in those fields. Winged males and females begin to fly to overwintering hosts in mid-August. The buckthorn aphid is a fairly efficient vector of PVY (11,14) (see also Singh & Boiteau, these proceedings) but a poor vector of PLRV (11).

Green Peach Aphid

The green peach aphid in warmer areas of Canada, including southern Ontario, overwinters as females on weeds and shrubs in ditches and as eggs on peach (Prunus persica (L.) Batsch), Canada plum (P. nigra Ait.) and black cherry (P. serotina Ehrh.). In mainland New Brunswick, there are no peaches and eggs are rarely found on Canada plum (6). This species has been found to overwinter as eggs on Canada plum in northeastern Maine, however (12). This aphid colonizes New Brunswick and, probably, the whole Atlantic region of Canada from outside and, therefore, develops later in the season. Occasionally, green peach aphids will appear on potatoes early in July. We believe that most of these early summer populations come from greenhouses or bedding plant stocks where they build up early populations. Generally, winged forms are not seen until after mid-July (4). Every year, winged green peach aphids move into New Brunswick and neighboring provinces from other areas from early August to early September. Since it is the most important vector of PLRV and an efficient vector of PVY, it is this late flight which is of concern in the seed potato production areas of N.B. and P.E.I.

Foxglove Aphid

The foxglove aphid is primarily a greenhouse pest and is seldom found on potatoes in New Brunswick. It may be more common on potatoes in parts of southern Ontario (M.K. Sears, personal communication). This species can spend the winter either in the egg stage on plants that remain green all winter outdoors, e.g. foxglove (Digitalis purpurea L.), plantain (Plantago maritima L.), clover (Trifolium pratense L.), hawkweed (Hieracium spp.) and strawberry (Fragraria sp.), or as nymph-producing females on potted plants and bulbs in protected places (7,18). It is rarely found in any abundance on potatoes and usually inhabits the leaves close to the ground. This aphid can transmit PLRV but not PVY (14,18), however, its scarcity on potatoes appears to rule out any significance as a vector.

APHID MONITORING PROGRAMS

Annual programs to monitor the activity of potato-infesting aphids and to provide a warning or "Aphid Alert" service to potato producers are currently carried out in New Brunswick, Prince Edward Island and, to a lesser extent, in Quebec. Some small scale monitoring has been conducted in research plots near London and Harrow in Ontario and local potato growers have been provided with information at critical times (M.K. Sears, personal communication). In Nova Scotia, yellow pan traps were formerly used to monitor potato aphids but this program was dropped a few years ago due to a shortage of summer help. Although 10 yellow

Table IV - Summary of Aphid Monitoring and Management Programs for Potatoes in Eastern Canada

	Ontario	Quebec	New Brunswick	Prince Edward Island	Nova Scotia
1. Aphids of Concern	green peach common potato foxglove	green peach common potato	green peach buckthorn common potato	green peach buckthorn common potato	green peach
2. Areas Monitored	SW Ontario-London -Harrow	Lower St. Lawrence Valley - nr. Rivière -du-Loup	Upper Saint John River Valley & Fredericton	province-wide - 5 districts	Annapolis Valley (Kentville area)
3. Monitoring System	-counts on plants	-2 suction traps-12 m -1 suction trap - 1 m (formerly - yellow pans for 10 years)	-yellow pans - 80-90 fields -counts on plants - 35-40 fields -1 suction trap- 12 m	-yellow pans-45 fields -counts on plants - govt. trial plots	-yellow pans - 10 (strawberry nursery fields)
4. Warning Service	-none - except reports from Res. Stations - London & Harrow	-none - generally few aphids trapped aphids identified after season	-available to all growers via code-a-phone -weekly reports to growers with traps or monitored plots -phone grower when 1st GPA trapped -information given to seed inspectors	-trap results sent to district offices -area information available via telephone -phone growers when GPA trapped -bulletins to radio	none - trapped aphids identified after season (former program dropped 2 yrs. ago)
5. Aphid Control Methods	-Alliston area - 75% use granular insecticide; others use 5-7 foliar sprays for beetles & leafhoppers also -Southwest - foliar sprays only (early season crop)	-sprays for CPB control potato aphid -may use 1 spray for green peach aphid -10% use granular insecticide (seed)	-granular insecticide plus 1-2 foliar sprays or foliar sprays only	-40-50% use granular insecticide plus foliar sprays when required; others use foliar sprays only	

pans are operated in strawberry nursery fields in the Kentville area, the catches are identified only after the trapping season (H.B. Specht, personal communication). Aphids are apparently not a problem on potatoes in Newfoundland. No monitoring is conducted and no insecticides are applied (W. E. Kayler, personal communication).

Table IV provides a summary of potato aphid monitoring/management programs and techniques employed in the eastern provinces of Canada.

APHID MONITORING SYSTEMS

Field Monitoring

This system involves periodic counting of aphids on potato plants in the field. In New Brunswick, weekly counts of aphids are made every season in 35 to 40 commercial potato fields in the major production area of the Upper Saint John River Valley. In each field, 30 potato plants are selected at random every week in a plot area about 30 m square. One top, middle and bottom compound leaf per plant are examined for aphids and the numbers of all stages of each species are recorded. In additon, the presence or absence of the Colorado potato beetle, Leptinotarsa decemlineata (Say), in the field is noted and a terminal leaflet on every second sampled plant is inspected for feeding damage of the potato flea beetle, Epitrix cucumeris (Harris).

The above data are entered into a computer program in the field, using a portable microcomputer. An individual report is generated for each field immediately after sampling and is given to the grower to inform him of insect pest population levels. This information can be used by the producer in making management decisions. It also provides the extension specialist with a basis upon which to formulate control recommendations. The report displays graphically the weekly change in the total aphid population since plant emergence and indicates the dates on which insecticides were applied. In this manner, the grower receives an indication of the effect on the aphid population of the insecticide chosen and the timing of application.

The New Brunswick program has always encouraged the use of systemic insecticides at planting in order to prevent the establishment and build-up of aphid populations early in the season. This could be particularly important in localities where green peach aphids can survive the winter inside greenhouses and infest nearby potato fields in the spring. In any case, large early populations of aphids (e.g. common potato aphid) which might affect potato yields in some years are avoided with systemics. In addition, there is a greatly reduced production of winged adults of all potato-infesting species which could fly to other plants or fields and spread PLRV or PVY. Growers who elect to use only foliar insecticides are advised, in general, to spray when a sudden and rapid increase in aphid numbers is observed early in the season or, in normal seasons when population development is slower, when the production of winged forms begins. This occurs usually at or after blooming. For more precise management of aphids during the growing season, the threshold levels shown in Table V have been suggested (2).

Table V - Threshold Levels Requiring Control of Aphids in New Brunswick*

Species	Aphids/Plant (#)		Infested Plants (%)	Aphids with Wingpads (%)
Macrosiphum euphorbiae				
July	50	and	40	
End July - Aug. 10	50	and	60	unless 5
Myzus persicae				
June - Aug. 21	25	and	10	
Aphis nasturtii				
Aug. 10-20	150	and	80	

*From Boiteau (2).

In addition to providing information on pests in specific fields for individual producers, data generated by the field monitoring program are used to compose timely general pest advisories and appropriate recommendations for the entire potato industry in the region. These are made available in a daily code-a-phone message and, occasionally, are disseminated via letters or the news media.

Aerial Monitoring

The use of yellow pan water traps is a well known technique for detecting flights of alate potato-infesting aphids. In New Brunswick, yellow pans have been used in commercial potato fields every summer since 1973, primarily to monitor inflights of the green peach aphid (4,8). During the 1986 season, a total of 86 yellow pans were operated in New Brunswick; 36 of these in table and processing fields in the field monitoring program, and 50 in seed potato fields. In Prince Edward Island, 45 traps were used on elite seed potato farms only (B.N. Craig, personal communication).

For the past seven growing seasons, the New Brunswick program has been using a custom-made yellow trap of molded plastic (Fig. 1). The pan measures 55x44x7 cm and has a plastic base attached so that its upper edge stands 25 cm above ground. It is painted black on the outside and on the upper edge to increase the contrast with the surroundings and to eliminate the need for a large ground space around the pan. Two holes 1 cm in diameter are drilled along the top of two sides to ensure that excess water from rainfall can run off without overflowing the tray. The interior of the pan is painted "buttercup yellow" (British Colour Council 53). After several seasons of field exposure, the colour has remained stable. When empty, its light weight facilitates handling and when filled with water (and weighted in the base), the trap is stable enough to resist most winds. A single trap is placed in potatoes at least 15 m from the edge of the field. Early in the season, the trap sits between the rows but is later moved on top of a row to approximate canopy height. The traps have proven to be sturdy, easy to clean and maintenance free.

In New Brunswick, insects are removed from the yellow pans twice a week. Aphids are sorted from each sample and the potato-infesting species are identified. Each participating grower receives a report listing the species found in each sample from his trap. When green peach aphids first appear in a sample, the producer is notified by telephone. Subsequently, a computer-generated map indicating the locations of green peach aphid catches is sent every week to each cooperator and also to district seed potato inspection offices of Agriculture Canada. When a total of more than five green peach aphids have been caught cumulatively in any one trap, the grower is warned to kill down his potatoes within 10 days, if possible, to prevent any leafroll infection from translocating to the tubers. A cumulative catch of more than five green peach aphids was found to be the threshold level for spread of PLRV (9).

After the beginning of the annual green peach aphid flight into New Brunswick potato fields, a special Topkill Committee composed of producers, extension specialists and seed potato inspectors meets to establish dates by which topkill must be started by all seed growers. The dates are based on data from the Aphid Alert Program, current disease levels, and on yield potential and virus susceptibility according to variety. The federal inspectors ensure that all seed potato producers comply with the mandatory dates.

For the past five years since the establishment of the Topkill Committee, leafroll levels in New Brunswick seed potato crops have remained very low. This is due largely to the quality of the seed planted and to relatively low numbers of green peach aphids flying into the area during those seasons. However, it is believed that mandatory topkill dates have ensured maximum freedom from PLRV in the Province. In some seasons, early topkilling may also have limited the spread of PVY. The concept of mandatory dates for topkilling has gained generally favourable acceptance by seed producers, in part because they recognize the quality control aspects and also because they see that all growers are placed on a relatively equal footing with respect to crop yields. Those who submit to the temptation of extending crop growth for a higher yield at the risk of increased virus spread, have their seed dropped to a lower class in the certification system.

RECENT DEVELOPMENTS IN APHID MONITORING

Suction Traps

Large 12.2 m high suction traps of the type developed at Rothamsted Experimental Station in England (17) have been used to monitor aphid migrations for many years in several countries of western Europe. More than 35 of these traps now exist in Europe and there is a network of 23 in the United Kingdom alone. They are used in those areas primarily to monitor cereal-infesting aphids, potato-infesting aphids, and a few other migrating pest insects. These traps have several advantages over the commonly used yellow pan water traps or yellow sticky traps. They have been standardized to provide a constant and quantitative sampling technique in all conditions of weather, wind speed and light. Accurate information on the aerial density of aphid species can be obtained since the catch can be related to a given volume of air sampled over a given period of time. Since they do not require a "decision" by an aphid to fly to them, suction traps sample aphid species (e.g. some cereal aphids) which are not attracted to yellow and, therefore, provide a more complete picture of the aphid fauna in the area. It is also reported (16) that the sample of the aphid fauna obtained with these traps is valid for an area within a radius of 80 km from the trap.

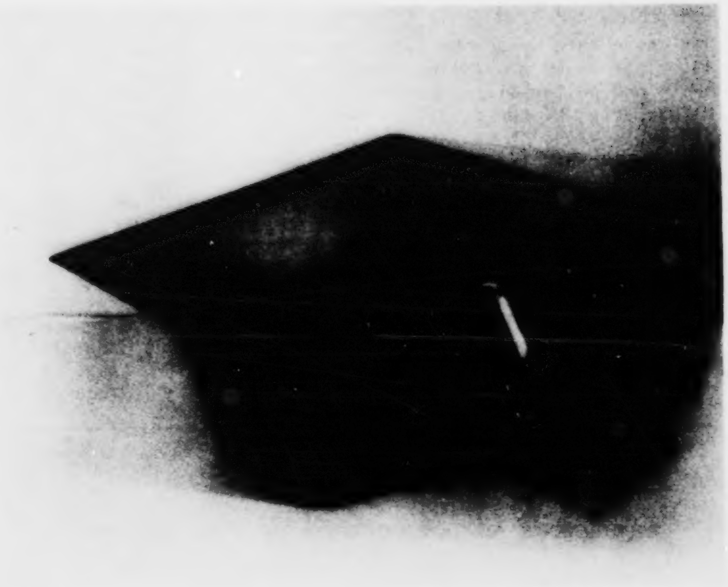
Two 12.2 m Rothamsted-style suction traps and a smaller 1 m Johnson-Taylor trap have been operated in Quebec since 1984 (5). Although established primarily for a general survey of air-borne aphids, they have been used to monitor flights of the green peach aphid. The 1 m trap and a 12.2 m trap are located in seed potato production areas near Rivière-du-Loup, however, the data are apparently not used for short term decisions since there is a delay in having catches identified (C. Cloutier, personal communication).

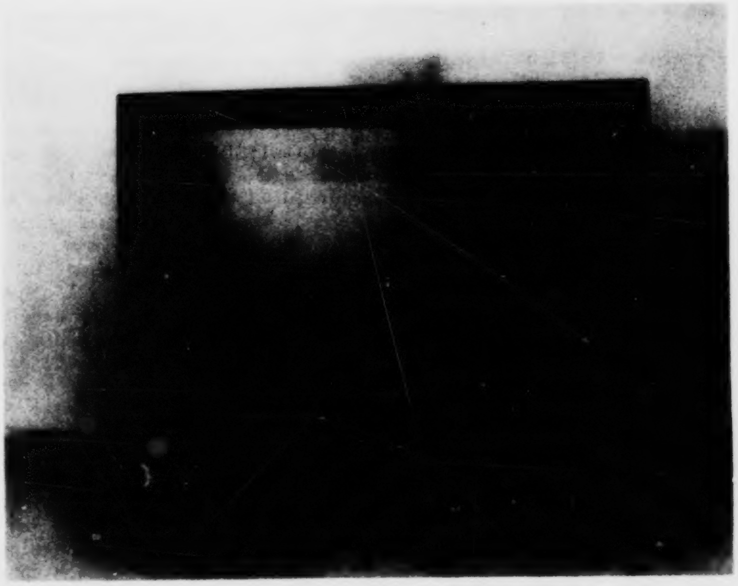
A 12.2 m Rothamsted trap identical to those in Quebec has been installed at Wicklow (five km north of Florenceville), New Brunswick and began operation during the 1986 season. Green peach aphids were first caught in the suction trap on August 6th, nine days after the first green peach aphid appeared in a yellow pan trap in the region and one day before the first cumulative catch of more than five green peach aphids in a yellow pan. It would appear, therefore, that the yellow pan trap network may be better at detecting the start of green peach aphid flights, however, this suction trap is being evaluated primarily as a tool for monitoring migrations of other aphid species which may be vectors of PVY.

Forecasting Inflights of Green Peach Aphids

Boiteau and Parry (4) showed that, in New Brunswick, yearly variations in the timing of the first cumulative catch of more than five green peach aphids in a yellow pan trap can be simulated by the thermal summation of 1188 degree days (above 4°C) and forecasted by regression on the timing of first inflights. Analysis of 10 years of pan data from the Aphid Alert Program indicated that, in 80% of the years, the first green peach aphid catch occurred in the northern part of the potato belt instead of in the consistently warmer southern part. This supports an earlier statement (6) that the green peach aphid rarely overwinters in the egg stage on Canada plum (Prunus nigra Aiton) in New Brunswick.

In light of the above findings, we consider it possible to streamline our program by operating fewer yellow pan traps for a shorter period of time (July 17 to the first green peach aphid catch) and in a smaller area (the northern region), just to detect the beginning of flights. The date of the first cumulative catch of more than five green peach aphids could then be forecasted using the regression of dates for





the cumulative catches on the dates for first yearly catch for the years 1974-83. This would provide an interval of about two weeks in which to make decisions on topkilling for the control of PLRV. This conclusion is also supported by the results from the past three growing seasons shown in Table VI which compares actual and forecasted dates for the first cumulative catch of more than five green peach aphids.

Table VI - Actual vs Forecasted Yellow Pan Catches of Myzus persicae in New Brunswick*

Year	Date of First Catch	Date of First Cumulative Catch ≥ 5	
		Actual	Forecast
1984	July 31	-	Aug. 16
1985	July 22	Aug. 6	Aug. 4
1986	July 28	Aug. 7	Aug. 11

*Boiteau & Parry, unpublished data.

REQUIREMENTS FOR IMPROVED APHID AND VIRUS MANAGEMENT

Although aphid and virus management programs in eastern Canada have, no doubt, helped to educate and assist producers in growing higher quality seed potatoes and, possibly, in achieving higher yields of better quality table and processing potatoes, there are still some gaps and weaknesses in the management packages available. One weakness is the lack of knowledge on the effect of the potato-infesting aphids on tuber yields. While it appears that potato plants are most sensitive to aphid feeding from the nine leaves stage up to bloom (3), the economic threshold levels for aphid numbers are not known. It is likely that these would be difficult to determine in Atlantic Canada where aphid populations on potatoes are usually relatively low. However, if we are to promote more efficient use of insecticides and the elimination of unnecessary applications, it would be useful to have more precise action thresholds for aphid control early in the season. This would permit improved timing of sprays and, possibly, reduced costs for the production of table and processing potatoes at least. Although some banded systemic insecticides provide good to excellent control of aphids early in the season, many growers avoid them because they are expensive and one of them, aldicarb, has been found to contaminate ground water in some areas (see Martel, these proceedings). New management alternatives involving changes in cultural practices or the introduction of other methods to enhance natural controls of aphids (see Boiteau, these proceedings) should also help to reduce growers' present dependence on chemical pesticides. For seed producers, it would be very beneficial to have more precise management recommendations regarding the control of aphids which may spread the mosaic viruses, PVY and PVA. The important vectors of these viruses, however, have not all been identified and the critical periods for their spread are not well established (see Singh & Boiteau, these proceedings). The importance of the green peach aphid in spreading PLRV is well established and reliable monitoring techniques are in use but we are not able to forecast the actual hazard of leafroll transmission in relation to the density of aphid flights. Unless the sources of the main summer migration of green peach aphids are determined, it will remain very difficult to assess the proportion of the population carrying PLRV (see also Frazer, these proceedings). Knowledge of these sources would permit improved forecasting of aphid flights (4), an evaluation of inoculum levels in those areas and, as a result, a better assessment of the potential for infection of our potato crops with leafroll. This could have important consequences for the economics of seed potato production since the date of topkill has a great effect on tuber yields. Furthermore, if sources of green peach aphid flights were identified, it might be possible to reduce aphid migrations through cooperative programs to remove host plants or, at least, to control the aphids on those hosts prior to the production of winged forms.

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APHID AND VIRUS MANAGEMENT IN POTATOES IN BRITISH COLUMBIA

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ABSTRACT

The size and economic significance of the potato industry in British Columbia is described. Although the industry is comparatively small, the effort and methods used to ensure virus-free production of potatoes are similar to those used elsewhere. Major concern and most research is directed to the luteoviruses, potato leaf roll virus (PLRV) and beet western yellows (BWYV). Although 5 species of aphids colonize potatoes, control is primarily directed at the green peach aphid because it is the most efficient vector and is ubiquitously present. The relative importance of each species of aphid infesting potatoes varies throughout the world but again, monitoring methods and rationale are similar.

The monitoring program, developed to aid in setting top-kill dates for seed potato producers is described. The incorporation of new, more sensitive and accurate virus detection technology is alluded to and its role in future monitoring programs is discussed.

RESUME

L'industrie de la pomme de terre en Colombie Britannique et son importance économique sont décrites. Bien que cette industrie soit relativement petite, l'effort et les méthodes utilisées pour assurer la production de pommes de terre libres de virus sont similaires à celles utilisées ailleurs. Les virus de l'enroulement de la pomme de terre (PLRV) et de la jaunisse occidentale de la betterave (BWYV) préoccupent le plus et font l'objet du plus de recherche. Bien que cinq espéces de pucerons colonisent les pommes de terre, le contrôle est dirigé principalement contre le puceron vert du pêcher à cause de sa distribution et de son efficacité supérieure comme vecteur. L'importance relative de chaque espèce de puceron infestant les pommes de terre varie de par le monde mais, encore une fois, les méthodes d'échantillonnage et leurs raisons d'être sont similaires.

Le programme d'échantillonnage établi pour aider à déterminer les dates de défanage pour les producteurs de pommes de terre de semence est décrit. La possibilité d'introduire une nouvelle technologie de détection des virus, plus sensitive et plus précise est esquissée et le rôle de cette technologie dans les programmes de surveillance à venir est discuté.

INTRODUCTION

Past research and present programs of technology transfer provide potato growers with planting stocks free of almost all known diseases. Keeping potatoes in that pristine state whether for use as seed, processing or table stock demands an integrated effort that currently does not exist. While Integrated Pest Management is not the topic of my talk today I cannot pass up the opportunity to mention it to this audience because so many of the disciplines and interests that need to be integrated are represented here today. True Integrated Pest Management of Potatoes will remain a fuzzy futuristic dream until all who have an interest in the crop share their knowledge, experiences and frustrations with each other. I work as part of a team that includes pathologists, virologists, inspectors, extension workers, growers groups, individual growers, private pest management consultants and many unsung heroes, the students who invariably do most of the boring routine work with humor and eagerness.

Important specialists not currently involved in the B.C. program are agronomists, physiologists, meteorologists, economists and potato breeders. It will probably never be possible to have all necessary specialists at one location, but far better and easier communication between specialists is possible and imperative.

A potato tuber is assaulted by insects and pathogens the moment it is placed in the ground or earlier if it becomes contaminated in storage or handling. To me the miracle is the list of ailments that potatoes have complete resistance to, not the rather short list of those that evade the plant's defences. My role as an entomologist is to find ways to prevent re-infection of potatoes by virus diseases carried by aphids.

The control of viruses in potato crops grown in temperate North America is very much a matter of preventing access to and colonization of aphids when the aphids are likely to be carrying viruses. An entomologist's job is to predict or at least forewarn of major aphid flights in sufficient time for potatoes grown for seed to be top-killed or for prophylactic residual sprays to be timed to limit waste and undue side effects (1, 8).

THE B.C. POTATO INDUSTRY

Over 65,000 tons of table stock and 2,000 tons of seed potatoes are produced in B.C. by 150 growers on 7000 acres of land (9t/acre). The industry generates $17 million or about $2,400 per acre annually. Over 90 percent of seed production is localized in the alpine Pemberton Valley 150 km from other potato production areas. The short growing season and isolation of Pemberton is ideal for seed potato production but land for that use is limited. Only 0.5% of seed potatoes in B.C. are produced in the Fraser Valley where most production is currently used for fresh and processing sales (D. Kirkham, Agricullture Canada, FP&I, pers. comm.).

Current research is directed at improving the quality of seed potatoes generally but specifically at determining if seed production could be increased in the Fraser Valley while retaining the disease free quality currently attained in Pemberton. Twenty years ago, a sugar beet seed industry was located down wind of the potato growing areas in the Fraser Valley. The biennial sugar beets, mostly unsprayed, produced enormous flights of Myzus persicae (Sulzer), the green peach aphids (GPA) that infested potatoes in early August (10). Despite the demise of the sugar beet seed industry, top-killing and spray schedules stayed the same. My first task was to determine if the timing of flights of GPA were different and hopefully later than they were 20 years earlier (11, 12). In the first three years of the program flights were 3-5 weeks later.

THE VIRUSES

My effort is primarily directed to PLRV because of its impact locally, nationally and internationally. A survey of the Fraser Valley showed the reservoirs of viruses infecting potatoes to be restricted almost exclusively to home gardens and commercial cull piles (Ellis and Vernon unpublished). My interest in BWYV was from the historical fact that the flights of aphids from sugar beets could not have been carrying PLRV, at least not PLRV as currently defined (4). Yet the arrival of these flights coincided with observed increases in the level of infection of potatoes by PLRV as it was defined without the aid of ELISA and monoclonal antibodies.

As a non-virologist I permit myself to hold perhaps heretical views about virus identity. I wonder if PLRV and BWYV are but the most conspicuous members of a complex similar to barley yellow dwarf virus (See Stace-Smith, these Proceedings). Such heresy would explain the significance of aphids on sugar beets to potato and the PLRV/BWYV mixed infection in plantain found by Peter Ellis.

THE VECTORS

Macrosiphum euphorbiae (Thomas), *Myzus persicae* (Sulzer), *Aphis fabae* Scopoli, *Aulacorthum solani* (Kaltenback), *Aulacorthum circumflexum* (Buckton) and *Rhopalosiphoninus latysiphon* (Davidson) colonize potatoes and all can carry one or more viruses. Most effort is expended on GPA because it is the most numerous on potatoes and the most efficient vector in B.C. The flight pattern of GPA is typical of an aphid that overwinters as eggs on *Prunus* trees and has many species of acceptable host plants in summer. GPA can survive and reproduce over the winter on several species of plants almost every year in B.C. Migrant aphids leave their hosts in April and early May. Potatoes are planted after May 1, weather permitting, and are not available for aphid colonization until late May or early June. Potato plants can become infested soon after emergence from the soil by aphids produced on any of over 90 species of local host plants. Only a fraction of the aphids that colonize potatoes in spring are likely to be carrying potato viruses. The recently developed monoclonal methods of detecting viruses in single aphids are far from routine. Until they are, we must assume that all GPA are equally likely to be carrying viruses.

CURRENT MONITORING PROGRAM

Southwestern B.C., where most potatoes are grown, is also the home of over 350 species of aphids (2). The first hurdle for monitoring is to develop the skill to differentiate GPA from the other 349 species. The predominant species on traps differ almost every trapping period. GPA rarely comprises more than 1-2% of the aphids trapped.

The components of the monitoring program consist of the trap, its method of use, number of traps per location, choice of fields, location of traps in the field, speed and accuracy of the identification of aphids and the method of communication of the results. All but the last is controllable and easy, but time consuming compared to ensuring that the results are used effectively by growers. The power of Agriculture Canada, Plant Health Division in certifying potatoes for export ensures that results are used but it also demands that results be rapidly produced and communicated to inspection staff.

We have many genera of aphids that are similar to but separable from GPA even at low power (x30) but only if the identifier has sufficient opportunity to compare similar species. We place traps in 2-3 locations beginning in May to provide fresh aphids to test and train discriminating powers of new staff and refresh abilities of experienced workers.

I have had years of experience with water pan traps and sticky boards of various constructions for other projects. I really wanted to develop a trap that could be returned to the laboratory and the aphids counted without removing them, thereby eliminating time consuming transfers and presorting of aphids from debris and other insects in the field.

Railroad board (a grade of poster stock) is painted with two coats of bright yellow paint with known reflective spectral qualities and is then cut into 10X30 cm rectangles. These are then painted with the commercial oil treatment, STP®, carried to the field where they are mounted with paper clips to a horizontal metal plate nailed to a 50 cm long stake. Much time was spent comparing various sizes, shapes, orientations and colors of traps. A horizontally mounted STP® trap is 3 times more attractive per cm^2 of trap area and requires half the time to service as water traps. Identifying and counting GPA on the STP® trap is somewhat faster than for water traps. Collection and handling is much faster and neater than for Stickem® coated traps.

Yellow pan water traps require a lot of maintenance: cleaning, repainting, carrying water to replace that lost by evaporation and thirsty birds and dogs, etc. Many bird species enjoy sitting, defecating, drinking, and bathing in water traps and several insectivorous species obviously consider water traps smorgasbords. Stickem® coated traps are just simply messy. Laboratories using Stikem® are easily identifiable because everything in them is stuck together.

The STP® trap, while not perfect, solves most problems. STP® is far less messy than Stickem® and, because it is less sticky, it captures fewer large insects than traps coated with Stickem® or similar polybutenes. STP® does wash off in rain but the effect is easily minimized by judiciously following weather reports and changing traps before and after a period of heavy rain.

Traps placed over fallow ground catch 2-10 times more aphids than when traps are placed near foliage. Plants appear to compete with the traps for the aphids' attention. A rather imperfect experiment indicated that traps placed 3 m apart did not interfere with each other.

Each year for the past 4 years, 10 traps were placed at least 10 m apart on fallow ground near potato fields in 6-14 strategic locations. Traps were changed weekly in the early part of the season and every 4 days starting in mid-July. Ten traps permits assessment of variability and when farm machinery mangles or fouls a trap, sufficient usable data remain. Finding safe places for traps that do not annoy growers was often very difficult. A piece of fenced fallow, waste land inaccessible to tractors and distant from wind deflectors is ideal but hard to come by in our fertile delta. Since the purpose of the traps is to assess the numbers of aphids in the air, traps can be placed where best coverage of a geographical area dictates, not only near potato fields.

About 100 traps can be processed in four hours by one person when aphids are rare or in 2 days when aphids are numerous. Results are expressed as number of GPA/trap/day of exposure to remove bias of varying exposure times in the field. When the numbers of GPA increase for two consecutive trap intervals in good weather, a major flight is beginning. Four traps at six strategic locations is sufficient for our major growing area (a flat delta) and that number of traps can easily be managed by one experienced person or two inexperienced people. Geography and knowledge of daily wind patterns determine the number and location of sites.

IMPACT

In positive moments, I think the monitoring program is perfect in that it provides the needed data in a timely and accurate manner. However, if the flight arrives before there is sufficient yield as occurred this year, topkilling would have resulted in yield loss with more severe consequences than the virus spread it prevents. In the previous 3 years, top-killing was safely delayed by 3-5 weeks from the pre-monitoring era and the Florida tests showed no increase in virus symptoms in the resulting tubers.

The program was operated in 1986 on 6 farms. Unusually inclement wet weather in May delayed planting by up to a month and an equally unusual long, hot summer resulted in massive flights of GPA in early August. To prevent access to the plants by the aphids by top-killing would have provided only 60 days growth and therefore an economically ruinous yield. The growth demands of the plant have priority over virus control. No PLRV was found in the Florida tests even though top-killing was not done until up to 6 weeks after the beginning of the flight of GPA. Flights of GPA have a limited role in spreading PLRV - provided - that the sources of inocuum are maintained at the present low levels. The rigorous, enforced certification program for planting stocks combined with the intensive inspections done in B.C. has reduced the potential of aphids to spread viruses.

EPIPHYTOLOGY AND THE FUTURE

Research Station staff now have monoclonal antibodies that can detect PLRV and BWYV in single aphids removed from traps or plants (5, 6). This ability will permit monitoring of the potential for infection, not just the numbers of aphids trapped. Monoclonal probes can also detect viruses in single leaves. These methods are being used, as you will hear, to find reservoirs of viruses to determine the pathways of the viruses from virus reservoirs to potatoes.

The goal of monitoring, when enhanced with use of monoclonal antibodies, will be to assess the severity of aphid flights and the proportion of those aphids that contain PLRV. Current monitoring programs must assume that all GPA are carrying viruses even though the very low rates of infection in the field show that only a small proportion of them actually are. The use of serological methods will permit sampling of alate GPA and determinion of their virus content. We hope that this will further delay the need to top-kill.

It may be unnecessary to monitor to determine when GPA flights begin; the time may be predictable from weather data (1, 9). The relationship is far from simple but I think it will be possible to predict within a week of when aphids may fly by using data from meteorological stations when properly adjusted for local micro-climate. Temperature is the single most important determinant of the rate of development of individual aphids and, therefore, of population increase, alate production, flight initiation and duration. We are working on this approach for strawberry aphids (3) because the aphids involved can not be identified without being cleared and mounted on microscope slides. Similar predictive approaches are being developed for many pests. The biology of aphids makes them particularly good subjects for computer modeling and realistic, accurate models of aphid population dynamics exist. To achieve the goal of predicting flight time and intensity, we will require much more basic research on the influence of weather variables on the flight behavior of aphids.

When the directive to top-kill is given, it would be useful to know the potential tuber yield at that time. Then, a grower could better decide if it were more cost effective to top-kill for seed or not top-kill and sell the tubers for table stocks. Simple but surprisingly accurate models of potato growth exist. I am testing and modifying one such model (7) to be integrated into the computerized integrated pest management package for potato pests in B.C.

We have all the tools needed to determine or predict the time of GPA flights, the viruliferous state of individual aphids, and the role of natural enemies and weather in aphid population dynamics. We now need to put it together into realistic, accurate and trustworthy computerized packages. That goal requires the same integration, communication and commitment as was required to get our species to the moon. The question is, is potato a sufficiently important crop to warrant that effort?

Irrespective of what you may think about computers, models and their use in pest and virus management, I can assure you that their greatest benefit to a researcher is that their use demands that data be gathered to estimate the variables known to be important. In this regard, there are several critical gaps in our knowledge about what I would call the field population dynamics of plant viruses in general. Are the well behaved domesticated viruses and aphids common to laboratory research truly representative of the field populations? I once gathered together 12 strains of PVY maintained by several virologists. None were transmissible by two lines of laboratory reared GPA. For ecological research, the use of laboratory strains of aphids is highly suspect. Parthenogenesis and inadvertent selection imposed by rearing produces aphids, which while perfectly adapted to rearing, bear little biological resemblance to the assemblage of clones in the field. I often wonder if similar selection of viruses for specific research purposes results in the same artificially-restricted variation. Monoclonal antibodies provide a tool to investigate this.

There is little virus information about rates of replication, within plant movement, accessibility to vectors and changes in host plant susceptibility to infection as affected by climate and agronomic variables. The new methods from serology and recombinant DNA research are exactly the tools needed to study the field ecology of plant viruses. They are almost to the stage where entomologists who botched every chemistry experiment required in university can use them.

Most pathological literature seems to define epiphytology (or epidemiology) as simply the pattern of disease incidence over time. To me, epiphytology is the study of the mechanisms that connect aphid population dynamics, meteorology, agronomy, virology and plant physiology that, in reaction to each other, result in a given pattern of disease incidence. I am excited and hopeful about tomorrow's epiphytology; budgets and staffing are another story.

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CONTROL OF APHID BORNE DISEASES: NONPERSISTENT VIRUSES

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ABSTRACT

Mosaics are nonpersistently-transmitted virus diseases that stubbornly continue to affect seed potato production in Canada in spite of all efforts to control them. The diseases are caused by or associated with viruses Y, A, X, M and S. More than 31 species of aphids are involved in their transmission throughout the world. The identification of aphids involved in the spread of mosaics in Canadian potato fields is the object of ongoing studies. Additional projects consider the role of internal and external virus sources and other variables in the epidemiology of mosaics. Finally, the paper reviews the status of the various control strategies in use or in development.

RÉSUMÉ

Les mosaiques sont des maladies à virus transmises de façon non-persistente qui continuent à affecter la production de pommes de terre de semence au Canada en dépit de tous les efforts pour les contrôler. Les maladies sont causées par ou associées aux virus Y,A,X,M et S. Plus de 31 espèces de pucerons servent de vecteurs de par le monde. L'identification des espèces impliquées dans leur transmission au Canada est en cours. D' autres projets considèrent le rôle des sources de virus internes et externes et d' autres variables dans l'épidémiologie de la mosaïque. Finalement, le papier passe en revue les différentes stratégies de contrôle disponibles ou en cours de développement.

INTRODUCTION

Any control strategy aims at an understanding of the principial components that interact to bring about the disease cycle. In aphid-borne potato virus diseases, at least four components need proper understanding. They are: 1) the viruses and the diseases they cause; 2) the aphid vectors; 3) the potato crop as the internal source of virus; and 4) the external sources of viruses. Interaction amongst these components and with the environment make such understanding a difficult challenge.

The diseases caused by nonpersistently-transmitted viruses in the potato crop are generally classed as mosaics. The type and severity of the mosaic depends on the particular virus or the combination of viruses involved. Along with blackleg and leafroll diseases, the mosaics were seriously affecting potatoes in Canada as early as 1922 (Table I) (1).

Although the incidence of mosaics was later reduced in seed crops throughout Canada, it has, nevertheless, persisted over the years (albeit in very low percentages) (Fig. 1). Compared to the persistently transmitted potato leafroll disease, the number of fields rejected due to non-persistently transmitted mosaic disease has been high from the 1920s to the mid-sixties (Fig. 2).

In New Brunswick, as in most of eastern Canada, mosaic has been a problem of seed potato production and in spite of various efforts to control it, it remains the most stubborn disease to date (Fig. 3). The present levels of mosaic have little or no effect on yield (36). Control techniques available are, therefore, quite satisfactory for tablestock and processing producers.

VIRUSES CAUSING MOSAICS

Recent surveys in New Brunswick (Singh and Hawkins - unpublished) and in Prince Edward Island (28,29) have indicated the involvement of mainly three viruses, i.e., potato viruses Y, A and X, alone or in various combinations (Table II). Potato virus S is also present in most plants showing mosaic, but does not seem to be the cause of mosaic. Potato virus M has been detected in seed stocks imported from Maine, U.S.A. and in the cultivar Shepody (Singh and Hawkins - unpublished).

The distribution of the viruses in the potato crop differs between provinces (Table II). The non-aphid-transmitted PVX was involved in 40% of the mosaics in P.E.I., but in only 18% of the cases in N.B. Potato virus Y was a more prevalent cause of mosaic in N.B. than in P.E.I. Potato virus A was involved in some cases in both provinces (Table II). There were also differences between cultivars in both provinces.

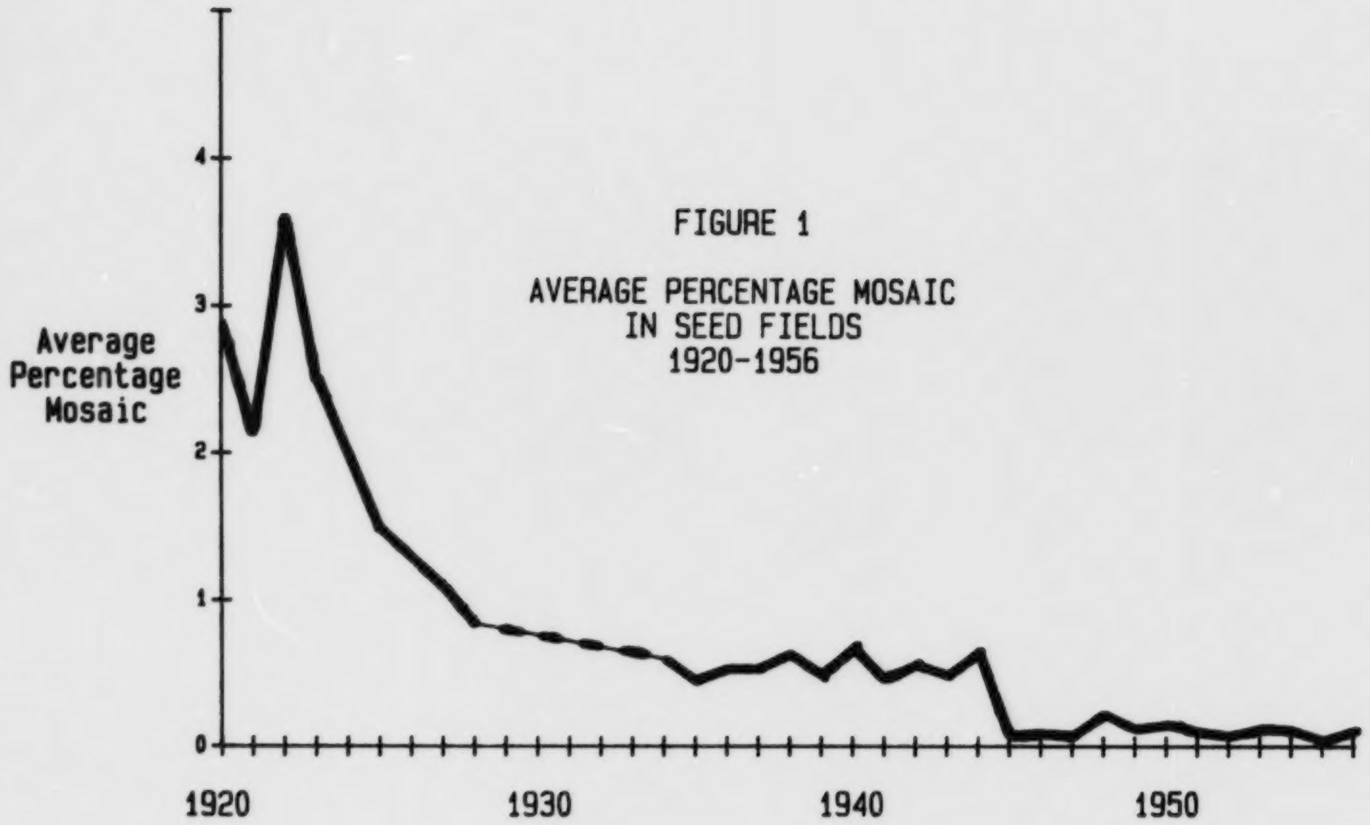
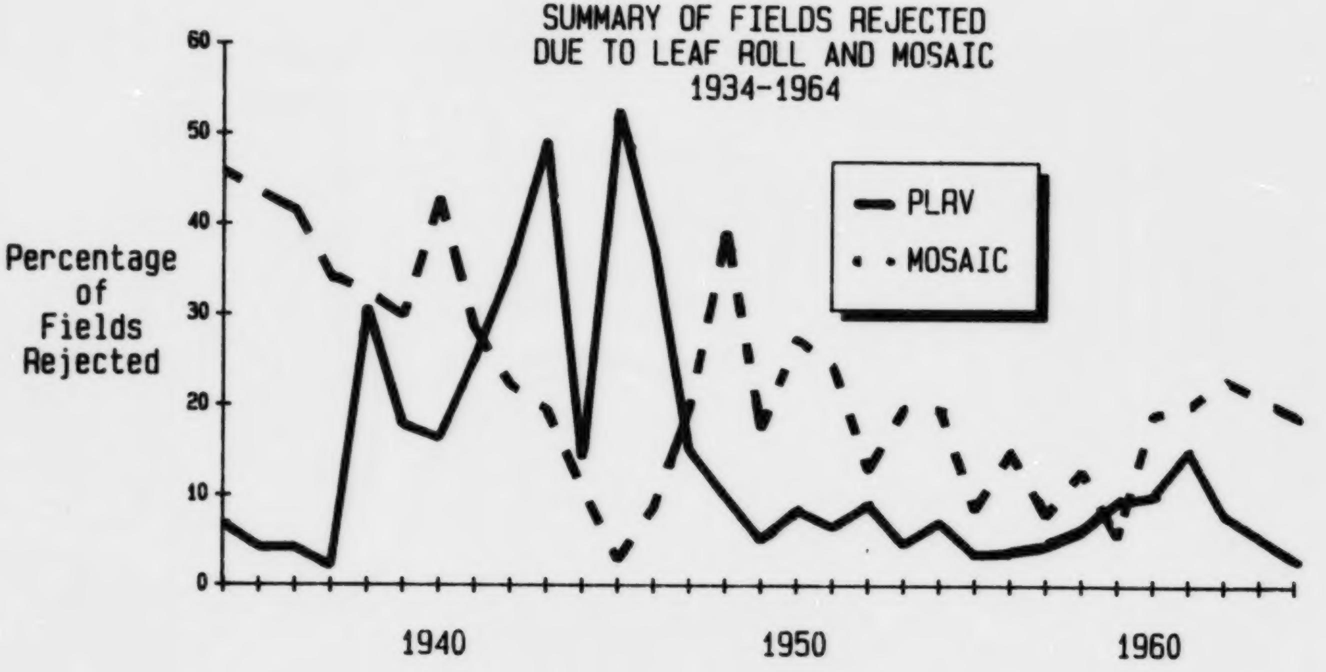


FIGURE 1

AVERAGE PERCENTAGE MOSAIC
IN SEED FIELDS
1920-1956

FIGURE 2



SUMMARY OF FIELDS REJECTED
DUE TO LEAF ROLL AND MOSAIC
1934-1964

FIGURE 3

SUMMARY OF FIELD INSPECTIONS
1938-1981

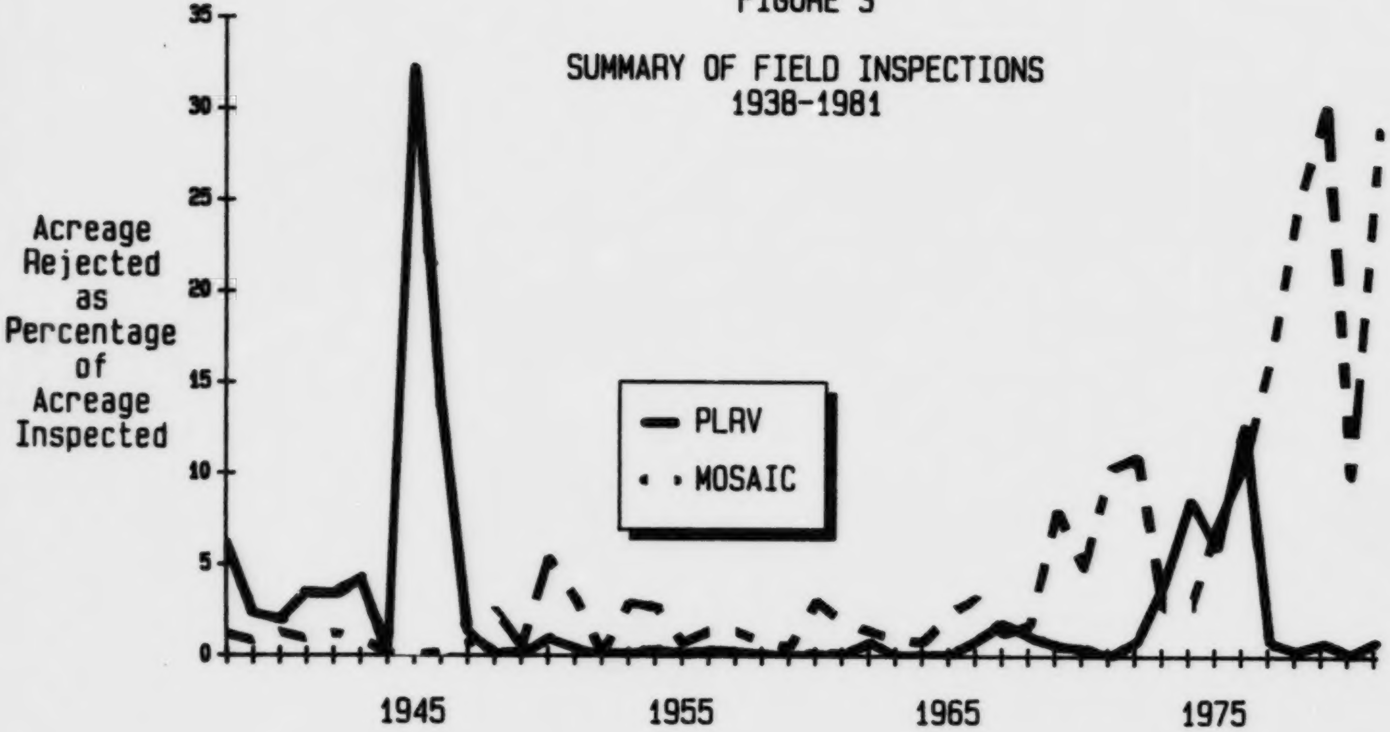


TABLE I

PERCENTAGE OF THE THREE MOST IMPORTANT DISEASES IN CANADIAN POTATO FIELDS INSPECTED FOR CERTIFICATION, 1922-1931[a]

Year	Number of fields inspected	Average percentage of disease found		
		Blackleg (%)	Leaf Roll (%)	Mosaic (%)
1922	3283	1.20	0.67	4.50
1923	2914	.62	.44	2.85
1924	5586	.50	.30	1.80
1925	4542	.65	.16	1.66
1926	4212	.37	.14	1.16
1927	8388	.35	.07	.79
1928	9610	.26	.11	.78
1929	8841	.21	.08	.91
1930	9707	.16	.28	.76
1931	11309	.12	.12	.54

[a] Data reproduced from Reference #1.

TABLE II

VIRUSES ENCOUNTERED IN SURVEYS OF MOSAICS IN NEW BRUNSWICK AND PRINCE EDWARD ISLAND PROCESSING POTATO CROPS[a]

	New Brunswick			Prince Edward Island				
	% infection			% infection				
Viruses detected	Russet Burbank	Shepody	Ave.[h]	Green Mountain	Red Pontiac	Russet Burbank	Shepody	Ave.
PVX	20	15	(18)	35	50	66	11	(40)
PVA	17	1	(9)	3	0	4	0	(2)
PVY	22	35	(29)	1	25	1	27	(14)
PVA+PVX	11	2	(7)	34	0	27	0	(15)
PVA+PVY	0	0	(0)	0	0	1	0	(0.25)
PVX+PVY	9	31	(20)	23	25	0	62	(22)
PVA+PVX+PVY	0	0	(0)	5	0	1	0	(2)

[a] The per cent infection is calculated from the data of McDonald (29) for P.E.I. and Singh and Hawkins (unpublished) for N.B.

[h] Average of all cultivars in brackets.

Potato Virus Y is a virus with long flexuous particles 730 x 11 nm, helically constructed with a pitch of 3.3 nm. Virus particles contain about 6% RNA which is single-stranded, and a protein of M_r 34,000. In the laboratory, PVY is easily transmitted mechanically to a narrow range of host plants, but in the field it is essentially transmitted by aphids. It occurs world-wide and causes economically important diseases in several Solanaceous crops (17).

In potato the virus may cause: a) mild to severe mottle, b) streak or leaf-drop streak, with necrosis along the veins of the underside of the leaflets, c) stipple-streak. There are three distinct strains: PVY° - the common strain; PVY^{N} - the tobacco necrotic strain, and PVY^{C} - the stipple streak strains. So far, only the first one has been found in this country.

The primary symptoms of PVY°, depending on the potato cultivar, are necrosis, mottling or yellowing of leaflets, leaf dropping, and sometimes premature death. Necrosis, which starts as spots or rings on the leaflets, may cause leaves to collapse and either drop from the plants or remain hanging from the stem (leaf drop streak). Secondarily infected plants are dwarfed and brittle, with leaves crinkled and puckered. Sometimes necrosis occurs in the foliage and stems. PVY° strains in mixed infections with PVX cause a very destructive disease called 'rugose mosaic' (17).

The differences between primary and secondary symptoms induced by potato virus Y are often indistinct because of the diversity of potato cultivars and combinations with other potato viruses. Moreover, symptom expression is affected by climatic conditions (17).

Potato virus A is also a potyvirus and contains RNA, with filamentous particles of 730 x 15 nm (16). It has a limited host range, mainly in the Solanaceae. The virus can be acquired and inoculated by the green peach aphid *Myzus persicae* (Sulzer) in a period of 20 seconds (26) and retained for 20 minutes (26). The green peach aphid can transmit potato aucuba mosaic virus when the source plants also contain virus A (14).

Potato plants may show a mild mosaic, roughness of the surface, waviness of the leaf margin, or no symptoms at all depending on the cultivar and on the weather. Some hypersensitive cultivars develop top necrosis when inoculated with PVA. Potatoes infected with potato virus A in combination with PVX or PVY may show crinkle symptoms. Potato virus A, left uncontrolled, could decrease the yield of infected potatoes by up to 40% (16).

Strains differing in virulence have been classed into four groups, i.e., very mild, mild, moderately severe and severe (26). Their virulence has been also correlated with their physical properties such as dilution end-point, thermal inactivation point and longevity *in vitro* (26) and also with their behavior in indicator plants (13). However, the relative importance and existence of these strains in Canada is not clear (40).

Potato virus X (see Singh, these proceedings).

VIRUSES LIKELY TO BE ASSOCIATED WITH MOSAICS IN CANADA

Potato Viruses M and S. Both viruses are members of the Carlavirus group and cause mild mosaic or latent infections. PVM has a sedimentation coefficient of 157S, a buoyant density in CsCl of 1.322 $g \cdot cm^{-3}$, and a nucleic acid content of 6.0%. The PVM genome is a polyadenylate single-stranded RNA (44). PVM causes various mottle, mosaic, crinkling and rolling symptoms in leaves and stunting of shoots. Host range is narrow. Several strains can be distinguished by the symptoms they induce in potato and in the indicator plants.

Potato virus S causes few or no symptoms and is carried by potato cultivars. Decreases in yields of 3-20% may occur (48). The host range is narrow. At least two strains are known on the basis of systemic reaction in Chenopodium species, the type strain and the Andean strain. The latter has not been recorded in Canada.

The spread of these potato viruses could be very rapid under field conditions. In a study in Germany using virus-free potato seed (47), 80% of the plants became infected by both viruses within three years. Additional potato-infecting nonpersistently-transmitted viruses are present in North America (43), but are not important in Canada (Table III). They have several aphid vectors.

TRANSMISSION OF NONPERSISTENT VIRUSES

Nonpersistent transmission of plant viruses is not rare. Of some 420 plant viruses described (18), about 150 are transmitted in a nonpersistent mode by aphids. This mode of aphid transmission is very rapid, requiring probes of only 5-60 seconds for the acquisition of the virus from infected sources. Fortunately, the ability to transmit the acquired virus is usually lost within 1-2 hours. However, it is thought that if the aphids are fasting they can retain the acquired viruses much longer (46).

Researchers first thought that the aphid stylets were somewhat accidentally charged with virus particles lost afterwards over a short period of time. Many studies, some recently, have concentrated on the stylets as a site of retention. However, the evidence collected is far from being conclusive. Other studies suggest a much more complex process. One hypothesis is that the protein coat of the virus plays an important role. Some sections of the alimentary canal of the vector would carry attachment sites specifically complementary to the protein coat of serologically related viruses. Other studies have shown the presence of a helper factor. This factor is not the virus but another element in infected plants that is essential for the aphid to acquire the virus. This factor may prevent inactivation of the virus by substances in the saliva of aphids or may ensure adherence of the virus to the attachment site in the aphid. A technique to demonstrate antigen on stylet tips based on enzyme-linked antigen distribution assay (25) was recently described (22).

TABLE III

POTATO VIRUSES TRANSMITTED NONPERSISTENTLY BY APHIDS[a]

Virus group	Viruses affecting potato	Particle morphology and size (nm)	Genome segments & sizes ($M_r x 10^6$)	Coat protein polypeptides and size ($M_r x 10^3$)	Number of aphid species involved
Alfalfa mosaic virus	Alfalfa mosaic	Baciliform 28-58 X18	3, linear SS-RNA 1.1+1.8+0.7	1, 24	14
Carlavirus	Potato virus M	Flexuous rod, 651	1, linear SS-RNA 2.5	1, 35.7	4
Carlavirus	Potato virus S	Flexuous rod, 657	-	-	3
Cucumovirus	Cucumber mosaic	Isometric, 29	3, linear SS-RNA 1.3+1.1+0.8	1, 24	60
Potexvirus	Aucuba mosaic	Flexuous rod, 580	1, linear SS-RNA 2.1	1, 18-23	-
Potyvirus	Potato virus A	Flexuous rod, 730	-	1, 30-31	-
Potyvirus	Potato virus Y	Flexuous rod, 730	1, linear SS-RNA 3.0-3.5	1, 32-36	31
Potyvirus	Potato virus V	Flexuous rod, 760	-	-	-

[a] Part of the data reproduced from References 18 and 44.

The high concentration of the virus in the infected plants greatly facilitates the acquisition and transmission of virus (2) and, in the case of potatoes, many popular cultivars can develop a high concentration of PVY when infected (41).

Aphid Vectors

Nonpersistent viruses are transmitted by noncolonizing, visiting aphid species (where aphids land and probe on the plants in the field, but take off almost immediately); by noncolonizing settling aphids (where aphids land, probe and feed on the crop for hours and sometimes for days, but do not reproduce); and by colonizing aphids (where aphids land and produce several generations on the crop, and where mixed populations of larvae, apterae and alates co-exist) (34). These viruses are of relatively low specificity for their aphid vectors.

About 31 species of aphids (20,30) have been identified as vectors of PVY throughout the world. Three of them are potato colonizing aphids confirmed as vectors in New Brunswick (38). Eight other species have never been recorded in New Brunswick (31) and are likely rare or nonexistant in the rest of the Atlantic region. Of the other twenty species, only three have been captured in New Brunswick potato fields (Boiteau, Singh, Parry and Pelletier, unpublished). A survey of the aphid fauna of potato fields has also revealed the presence of a number of aphid species whose efficiency as virus vectors is unknown. In our research, aphids captured in field plots at the initiation of PVY spread or during the development of the disease are considered potential vectors. Nine such species are suspected of playing a role in PVY spread in potatoes in this province (42). These aphid species are being tested to determine their intrinsic vector potential.

At least 7 species of aphids can transmit PVA: *Aphis nasturtii*, *Macrosiphum euphorbiae*, *Myzus persicae*, *Neomyzus circumflexus*, *Aphis fragulae*, *Aulacorthum solani*, *Brachycaudus helichrysi* (13,15,26).

Potato virus M is transmitted readily by *Myzus persicae* and less efficiently by *Aphis fragulae*, *Aphis nasturtii* and *Macrosiphum euphorbiae* (47).

Aphids (*Aphis nasturtii* and *Myzus persicae*) have been shown, in the laboratory, in Germany and in New Brunswick to transmit PVS but only at low levels, around 2.9%, even though spread patterns suggest the involvement of aphid vectors (47, and Singh, unpublished).

Although the known vectors of PVA, PVM and PVS are present in Canada, the vector effectiveness of the Canadian biotypes and their role in disease epidemiology has yet to be evaluated.

Methodology to Determine Intrinsic Vector Effectiveness

The intrinsic effectiveness of aphid vectors is determined by exposing non-virus carrying aphids to a diseased plant for virus acquisition followed by their transfer to a healthy indicator plant for virus transmission. The use of large aphid numbers per plant in early studies did not make it possible to differentiate clearly between aphids with different degrees of intrinsic vector effectiveness. Ideally, aphids are exposed and transferred one by one. This is the technique used in our laboratories.

In these tests, the indicator plant has traditionally been tobacco, with results automatically extended to potato. Recent tests with M. euphorbiae using both tobacco and potato indicator plants showed that the vector ability of an aphid can vary depending on the indicator plant used. In this case the aphid has minimal vector ability for PVY on potato but a definite one on tobacco (39).

The existence of various strains of viruses and biotypes of aphidssuggest that aphid vectors must be evaluated in each region.

Vector Effectiveness in the Field

To be an effective virus vector, an aphid must not only have some level of intrinsic vector effectiveness, but must also be present on the crop and move from plant to plant or from field to field.

The presence of potato colonizing species of aphids varies somewhat throughout the country. Winged green peach aphids reach New Brunswick July 26-29 and increase to significant numbers around August 8-11 (8). These data indicate that in spite of its high intrinsic vector effectiveness the green peach aphid can be responsible for PVY transmission only in August. In PEI, where the species is generally 1-2 weeks later, the transmission period is even shorter. In British Columbia, aphids can survive the winter and colonize the potato fields early in the season (49). In spite of these conditions favorable to the vectors, the spread of PVY is limited in the west of the country. This may be due to reduced sources of inoculum caused by the isolation of the seed-growing areas or due to the use of varieties less susceptible to PVY.

Buckthorn aphids can colonize the New Brunswick potato crop in mid-June spending as much as 8 weeks on the crop vs. 3-4 weeks for the green peach aphid. This longer period of contact with the potato could make the buckthorn aphid a more important vector than its intrinsic vector effectiveness of 19% (38) may suggest. Except for Quebec, this aphid is not common in the rest of the country (4).

Similar data on the seasonality of all other aphids with a demonstrated intrinsic vector effectiveness have yet to be assembled.

An understanding of vector dispersal also requires a knowledge of flight periodicities and the temperature thresholds for flight. These data were gathered for M. persicae, A. nasturtii and M. euphorbiae (5) (Table IV). The first vector is a morning flier and the second an afternoon flier because of its higher temperature threshold for flight. In spite of these differences, an analysis of temperature data in New Brunswick over the years shows that both species have a similar average number of hours available for flight per day (Boiteau, unpublished). It

TABLE IV

FLIGHT PERIODICITY, TEMPERATURE THRESHOLD AND TENERAL PERIOD OF POTATO COLONIZING APHIDS

Species	Flight periodicity		Temperature (C)	Teneral period (hours)
	Type	Mean time		
Myzus persicae	Unimodal	12:25 (4h 6m SD)	16-17	24
Aphis nasturtii	Unimodal	15:16 (2h 32m SD)	19	24
Macrosiphum euphorbiae	Bimodal	11:57 (2h 57m SD) 18:55 (1h, 5m SD)	16	24-48

TABLE V

RELATIVE INTRINSIC EFFECTIVENESS OF APTERAE AND ALATAE APHIDS AT TRANSMITTING POTATO VIRUS Y

Aphid species	Indicator plant	Per cent transmission	
		Apterae	Alatae
Macrosiphum euphorbiae	Potato	0.0	4.5
	Tobacco	30.0	23.0
Aphis nasturtii	Tobacco	27.0	23.0
Myzus persicae	Tobacco	47.0	64.0

TABLE VI

PERCENTAGE OF FIELDS REJECTED DUE TO MOSAIC, FROM THE TOTAL REJECTED IN NEW BRUNSWICK[a]

Year	Fields rejected due to mosaic from the total rejected (Per cent)	Fields certified (Per cent)
1965	15	87.02
1966	19	79.47
1967	11	86.59
1968	10	89.91
1969	34	86.69
1970	43	94.32
1971	48	87.75
1972	60	92.12
1973	18	91.44
1974	18	89.55
1975	34	90.42
1976	36	87.61
1977	91	89.66
1978	87	86.77
1979	88	86.17
1980	63	92.46
1981	80	87.1
1982	48	87.5
1983	88	88.0
1984	70	90.0
1985	29	88.0
1986	59	87.0

[a] Data received from Food Production and Inspection Branch.

seems that temperature should not be a modifying factor of the respective intrinsic vector ability of these two species. The very low intrinsic vector ability of M. euphorbiae is improved by the long period of time suitable for the flight of this species every day. Even so, its presence on the crop prior to the beginning of the spread of the disease suggests that it is not an important vector of PVY.

Vector Effectiveness of Apterous Aphids

After crop colonization, most of the aphid population consists of apterous forms. Based on data for PLRV, it has often been presumed that apterous aphids are intrinsically more efficient vectors than alatae. Studies at Fredericton suggest that this cannot be generalized between viruses or test plants. On potato, M. euphorbiae alatae are more efficient vectors of PVY (4.5%) than apterae (0%) but on tobacco, alate are less efficient vectors of PVY (23%) than apterae (30%) (39). Similarly, A. nasturtii alatae are less efficient (23%) than apterae (27%). In the case of M. persicae, alatae are more efficient (64%) than apterae (47%) (Table V) (38).

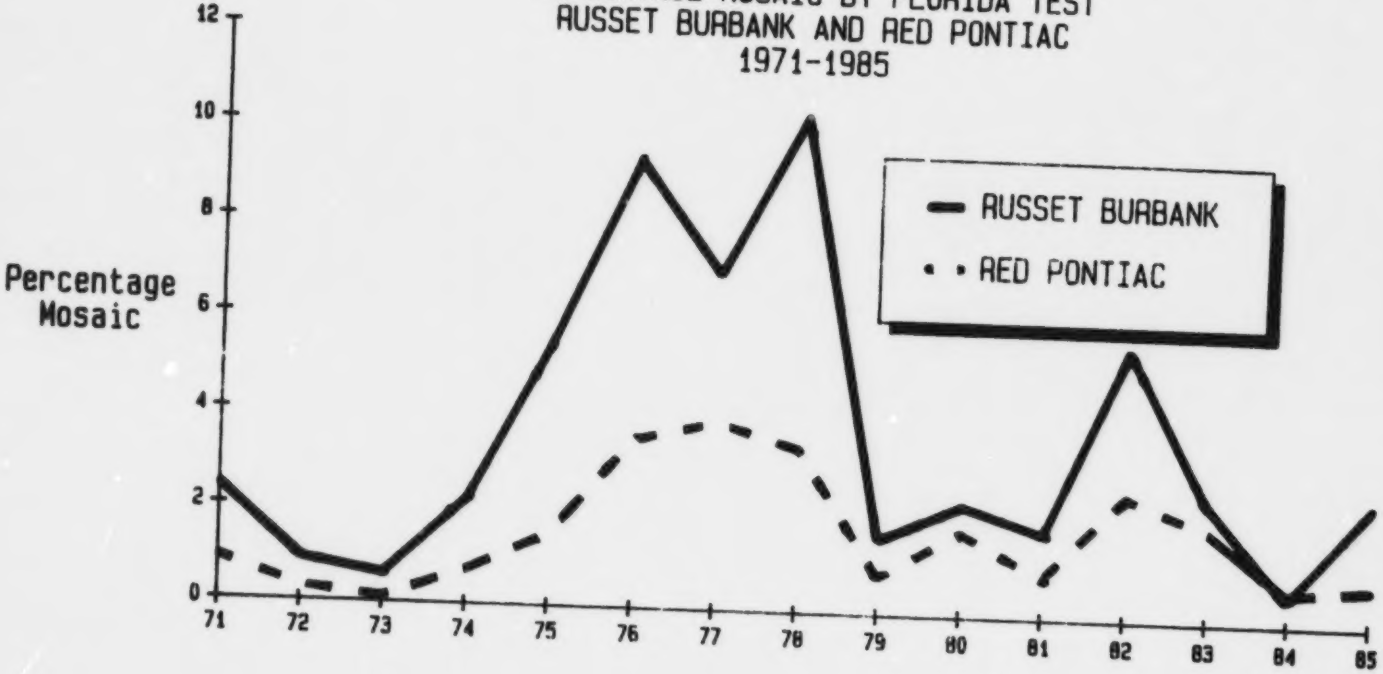
Early in the season, regardless of their intrinsic effectiveness, apterous aphids are not likely to be important vectors of PVY because of their low numbers and the very open canopy. Closed canopies probably favor the movement between plants. The behavior of the aphids is probably the next most important factor. It has been generally observed, for example, that the buckthorn aphid is reluctant to change position on the plant, decreasing its probability of interplant movement compared to the green peach aphid. This "behavioral mobility" of the aphid can be stimulated by external factors such as predators and insecticides (7).

Internal Sources of Viruses

Aphids moving within fields spread the viruses in proportion to the number of source plants available. Aphids moving between fields spread the viruses in proportion to the distance travelled and the number of source plants available. As depicted in Figure 2, mosaic-infected source plants have persisted throughout the years 1922-1964. With the increase in the acreage of susceptible cultivars like Russet Burbank, there has been a corresponding increase in the rejection of potato seed fields due to mosaic (Fig. 3). Although the percentage of fields passed for certification in recent years has remained fairly constant (79 to 94%), the main characteristic of the rejected fields has been the percentage of mosaic (Table VI). Looking at the postharvest "Florida" tests (which also detect late infection) for mosaic susceptible cultivars, it becomes clear that cultivars like Russet Burbank do harbour a high percentage of mosaic infection during the growing period (Fig. 4). It provides a virus source early on in the development of the crop. The number of mosaic source plants available in New Brunswick potato fields is sufficient to constitute a major internal source of virus for aphids.

FIGURE 4

PERCENTAGE MOSAIC BY FLORIDA TEST
RUSSET BURBANK AND RED PONTIAC
1971-1985



The External Sources of Viruses

Several weeds and other crops like tomato, pepper, and tobacco can serve as reservoirs of nonpersistently-transmitted viruses to the potato crop. However, (Singh, these proceedings) no weed hosts of PVY or PVA have been found in N.B. Other Solanaceous crops like tomato, pepper or tobacco, or weeds belonging to the genus Physalis, have been recorded as hosts of PVY in other countries (Singh, these proceedings). These plants are not widespread in Canadian potato-growing areas, but could serve as PVY reservoirs in some regions, such as Southern Ontario. Information on this aspect is needed.

CONTROL STRATEGIES

Plant virus diseases are seldom easy to control and many different approaches are employed in attempts to develop effective procedures for restricting or delaying the spread or to decrease the damage sustained after infection. A significant decrease in the amount of mosaic was achieved through the introduction of seed certification in the 1920s (Table I). However, with the increased use of susceptible cultivars, a combination of control measures has been developed here and elsewhere.

A. **Planting of clean seed** free from tuber-borne infection, with the lowest "Florida" readings or laboratory evaluation, is the most important step in the control of mosaic disease. Potatoes being grown from vegetative parts, there is a direct relationship between the buildup of disease and the years of continuous cultivation. The percentage of "seed" infected must be kept at a minimum to satisfy commercial requirements and to help restrain the future development of epidemics. Seed certification programs ensure the low infection rates of the "seed" crop.

B. **Avoidance of vector pressure.** It is best to grow the crop in periods in which vectors are absent or when their population density is low. Because of restrictive climatic conditions, this method is of limited value in Canada (see Boiteau, these proceedings). Green-sprouting of tubers to promote early emergence of potatoes and the resulting early growth and early mature-resistance would be desirable.

C. **Growing crops away from sources of infection.** The intensity of virus spread is affected not only by the number of vectors, but also by their distance from the target crop. In New Brunswick, the production of tablestock, processing and seed potatoes has historically taken place on the same fields. It is only recently that an isolated seed growing area was created in N.B. under the regulation of the N.B. Disease Eradication Act of 1979. This type of isolated seed growing area is also present in B.C., but not in other provinces.

D. **Insecticides.** Most insecticides have limited effects on PVY spread. They generally do not kill the aphids fast enough to prevent entirely the acquisition and transmission of nonpersistent viruses. The fast knockdown characteristics of pyrethroids gives them more effectiveness against the spread of virus diseases. Also, at sublethal concentrations, they affect the movement and the feeding behavior of aphids. This action can reduce the spread of PVY to some extent (19). These behavioral effects were confirmed in Canada for M. persicae and extended to A. nasturtii. Sublethal effects are, however, not limited to the pyrethroids (Lowery and Boiteau, unpublished).

Increased infection in treated fields is sometimes attributed to an increased excitation of aphids which probe and inoculate more. This is certainly not always true. At Fredericton, tests have shown that M. persicae and M. euphorbiae exposed to sublethal doses of aldicarb did become restless but also had a significantly reduced ability to probe and to fly, which should reduce spread (6). This indicates that insecticidal and noninsecticidal behavioral modifiers could be the important elements of integrated pest management programs.

E. **Spraying with mineral oils.** The discovery at Fredericton (12) that fatty substances inhibited the transmission of nonpersistent viruses by aphids led to the development of a mineral oil technology (9,10,11). Introduced in Canada, the technique was rapidly abandoned because of toxicity problems but recuperated by the Europeans (45). Canadian tests in the early 1980s confirmed that problems had resulted from the tank mixing of some fungicides with the oils. In spite of this, the technique remains marginally used, in great part due to the high cost of weekly applications. A better determination of the period during which PVY spread actually takes place might lead to a reduction in the number of sprays required. Otherwise, further improvements of this technique will likely await the resolution of the mode of action of the oil.

In Europe, the control of nonpersistent viruses on some other crops has been improved significantly by using the oil and a fast acting pyrethroid insecticide in combination (35). Similar work on potatoes has not yielded the same results (33). Even if it could be extended to potatoes, the high cost of pyrethroids combined with the oil is not likely to make this an economical technique on potatoes.

F. **Breeding for resistance.** Even though this strategy has potential, most of the popular cultivars in Canada are highly susceptible (3) and they develop high concentrations of PVY (41). Resistant cultivars have a great advantage as a basic component and it usually enhances the effectiveness of other control measures. Non-preference should perhaps be the most effective form of resistance to the vector for the control of nonpersistent viruses. Alternatively, the best combination of resistance may be one of the three types of vector resistance (nonpreference, antibiosis or tolerance), plus resistance to viruses. Resistance to viruses is generally more stable than resistance to other pathogens (24). Breeding for tolerance may be preferable resistance (see Tarn, these proceedings). Under consideration also is breeding of varieties with leaf trichomes which interfere with host finding (see Pelletier, these proceedings) or cultivars with low virus concentration (41).

G. **Antiviral factors.** Chemicals which interfere with virus infection and multiplication are called antiviral factors. Resistance against viral infection is induced by these chemicals which seem to activate the existing potential for this kind of response in the plant. Sodium salicylate is such a compound against TMV in tobacco plants. However, potted tobacco plants whose soil had been treated with Na salicylate did not show any resistance to necrotic potato virus Y (32).

H. **Aphid alarm pheromones, mulches, nets and whitewash sprays.** The release of aphid alarm pheromones should theoretically interferewith aphid landing and reduce the spread of virus diseases. However, European researchers observed no reduction in virus infection by alate aphids transmitting PVY to potatoes (21). However, transmission of PVY in pepper was reduced by it (34).

In Ontario, mulches of straw, sawdust, woodchips and corncob reduced the incidence of PVY in peppers (23). The author considers that this may be applicable to other vegetable crops. Mulches and nets have been found to be successful at interfering with aphid landing elsewhere (34). Recently, whitewash sprays (reflective materials) were shown to be 0-68% effective in reducing PVY incidence in potatoes in Israel (27).

LOOKING TO THE FUTURE

Canadian research on the control of PVY has persisted throughout the years and has succeeded in facilitating control of the disease satisfactorily for tablestock and processing potato producers. The oil spray technology has been accepted elsewhere on potatoes and extended to a variety of other crops where its usage is even more consequential than on potatoes. However, constraints on the seed potato industry have made it more and more important that PVY be better controlled. This will require an understanding of PVY epidemiology. The isolated research projects of the past are inappropriate to this challenging task where disciplines of virology, entomology and ecology need to be brought together.

The work on potato viruses and other nonpersistent viruses clearly shows that one cannot extrapolate from the laboratory to the field. More than ever before, studies will have to be conducted under field conditions. Support of a kind rarely available now is required for these long and laborious studies to take place.

Simulation models of PVY epidemiology are becoming available from American and European research teams (37). These models are still "primitive". Many parameters have had to be assumed. Canadian researchers must study these parameters (occurrence and behavior of vectors, prevalence of the different viruses, identification of virus sources, affect of the environment on viruses and vectors). Any opportunity of developing novel control measures should be pursued concurrently.

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CONTROL OF APHID-BORNE PERSISTENT VIRUSES

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ABSTRACT

For several years the only aphid-borne persistent virus known to infect potato was potato leafroll virus (PLRV), the virus responsible for potato leafroll disease. Recently, a second virus, beet western yellows virus (BWYV), has been implicated as a common component in the leafroll disease complex. There is some controversy as to the prevalence of BWYV in leafroll-infected potatoes - some published results indicate that it is common but recent tests in British Columbia, using highly specific monoclonal antibodies, suggest that BWYV rarely infects potato plants. Potato leafroll is one of the most serious diseases of potato. A variety of control measures has been devised, all aimed at reducing the incidence of the disease in those tubers that are used for seed. While there are many aspects involved in control, all are aimed at devising an effective seed potato certification system. Programs in place in Canada have been reasonably successful with the result that PLRV incidence is usually not a reason for rejection of fields entered for certification. The major problem with the control strategy is that it requires close monitoring of aphid populations. Future strategies, based on breeding for resistance and gene manipulation offer considerable promise.

RESUME

Le virus de l'enroulement de la pomme de terre (PLRV), responsable de la maladie du même nom, a été pendant longtemps le seul virus persistant transmis par puceron connu sur pomme de terre. Récemment, un deuxième virus, celui de la jaunisse occidentale de la betterave (BWYV), a été identifié comme une composante courante du complexe de la maladie de l'enroulement. Une certaine controverse existe quant à la prévalence du BWYV chez les pomme de terre infectées par l'enroulement - certaines publications indiquent que le virus est commun mais des essais récents en Colombie Britannique, utilisant des anticorps monoclonaux hautement spécifiques, suggèrent que le BWYV infecte rarement les plants de pomme de terre. L'enroulement est une des maladies les plus sérieusese la pomme de terre. Un bon nombre de techniques de contrôle ont été développées. Elles visent toutes à réduire l'incidence le la maladie dans les tubercules utilisées pour la semence. Bien que le contrôle tienne compte de plusieurs aspects, l'objectif principal est un système de certification de la pomme de terre efficace. Les programmes en place au Canada ont été raisonnablement efficaces. L'incidence du PLRV est rarement une raison pour refuser la certification des champs. Le principal problème avec la stratégie de contrôle actuelle est qu'elle dépend d'un échantillonnage suivi des populations de pucerons. Les stratégies futures, basées sur la résistance des plants à la maladie et les manipulations génétiques offrent un potentiel considérable.

INTRODUCTION

At first glance, the subject assigned to me appears to be reasonably straightforward. All that is required is an assessment of the world literature on the subject, a close examination of what has been published in Canada and establishing contact with research workers and potato certification officials in Canada to obtain their input. This is essentially the process that I have adopted in preparing this paper. The problem that I encountered is that there is anything but complete agreement as to which persistent virus or viruses are important and what control strategy is most likely to succeed. I therefore decided to attempt to answer two questions, namely (a) what persistent aphid-borne viruses should we be concerned about? and (b) what control strategies should be adopted? As with the identification and control of many other aphid-borne viruses, hard facts are often lacking and one has to rely to a large extent on unconfirmed observations, opinions and speculation. When these factors are blended together, one ends up with a mixture of science and science fiction. It is my hope that the science portion of this mixture outweighs the science fiction portion in this presentation. However, I shall leave it to you to decide that.

HOW MANY VIRUSES ARE INVOLVED?

Certainly, this is a critical question that must be answered. Are we talking about one virus, ... two viruses ... or several viruses? The answer to this question will vary depending upon whom the question is directed to. There are some authorities who would contend that there is only one persistent aphid-borne virus of any consequence that affects potato, namely potato leafroll virus (PLRV). After all, it has been known for many years as a problem in potato throughout the world. It is an accepted fact that it persists in the aphid vector and induces a disease known as "leafroll" in potato. This dogma held until about 6 years ago but is now being questioned in Canada and in other potato-growing countries. There are now a few scientific papers claiming that our simplistic view of the potato leafroll disease being caused by a group of closely related strains that together constitute PLRV is not correct and that a second virus, beet western yellows virus (BWYV), is a major component in a complex of viruses that is responsible for the potato leafroll disease.

You might ask, does it really matter whether there is a single virus or two or more viruses that together as a complex induce leafroll disease? After all, both causal agents are aphid-transmitted. Is this a question that may be of interest to the academic but of no practical significance? After all, both PLRV and BWYV are transmitted by the same aphid species so control measures directed at the vector should succeed equally well whether one virus or two viruses are involved. Well, the answer is not that easy. In fact, while the question is of academic significance, it is also important from the practical point of view. First, our potato certification program is based on an extensive testing program to ensure that the elite stock is virus-free. We are now relying on serological testing using antiserum prepared against PLRV for detection of the leafroll virus in the clones that are used for propagation. Is it possible that by adopting this test procedure, we could be missing those infections caused by another virus in the complex? Secondly, BWYV has a wide natural host range, involving many weed and crop species that are not considered to be natural hosts of "normal" PLRV. Is it possible that hosts of BWYV may serve as inoculum sources for a virus that is part of the leafroll complex?

SIGNIFICANCE OF BWYV IN THE LEAFROLL DISEASE

One thing all authorities agree on is that if more than one virus is involved in the leafroll disease, the causal viruses share many common properties and can be classified in the same virus group. At the present time, viruses that are sufficiently well characterized to be included in a classification scheme are divided into 28 groups. One of these is the luteovirus group (derivation of name: luteo: from Latin "luteus", from yellowing symptoms shown by infected plants). The main characteristics of the viruses assigned to this group are tabulated in Table 1.

Table 1. Characteristics of viruses belonging to the luteovirus group

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A. Properties of the particles

Nucleic acid: One molecule of ss-RNA, MW 2.0×10^6
Protein: one coat polypeptide, MW 24×10^3
Morphology: Isometric particle, ca. 25 nm diameter
Antigenic properties: Strongly immunogenic; most members are serologically related

B. Replication

Confined to phloem tissue of infected plants

C. Biological aspects

Host range: varies with members; some infect wide range of species; others restricted to a few plants
Transmission: persistent by aphid vectors; virus does not replicate in vector; pronounced vector specificity among some virus isolates; none transmitted by mechanical inoculation; aphids rendered inoculative by injection; several members associated with dependent virus transmission by aphids from mixed infections

D. Members

Type member: barley yellow dwarf virus (BYDV) MAV isolate
Other members: 14 known, 3 probable, 16 possible

The two viruses in the luteovirus group that are of particular interest when the persistent aphid-borne viruses affecting potato are considered are PLRV and BWYV. Since the relative significance of these two viruses is going to be examined, it may be helpful to start by comparing their properties (Table 2).

Table 2. Comparison of properties of potato leafroll virus (PLRV) and beet western yellows virus (BWYV)

	PLRV	BWYV
Host range:		
	Narrow - few natural host species	Wide - over 100 species
	Most hosts in Solanaceae	Not common in Solanaceae
	Brassica pekinensis thought to be a non-host	Many *Brassica* hosts
Vectors:		
	Transmitted by several aphids	Transmitted by several aphids
	Myzus persicae most important	*M. persicae* important vector
	Macrosiphum euphorbiae good vector of tomato strain	
Serological relationships:		
	Closely related to tomato yellow top, tobacco necrotic dwarf and Solanum yellows	Closely related to beet mild yellowing and turnip yellows
	Related to beet western yellows, beet mild yellowing and bean leafroll	Related to potato leafroll

It is evident from the summary of properties listed in Table 2 that PLRV and BWYV have far more similarities than differences. The viruses share the same vectors and, under field conditions, the green peach aphid, *Myzus persicae* Sulzer, is the most efficient vector of both viruses. The natural host range shows some differences. In general, if a virus is isolated from a solanaceous plant it is more likely to be PLRV than BWYV. However, host range and host reaction differences are a tenuous basis upon which to differentiate between two viruses because a change in the vector efficiency or intensity of vector pressure may result in a low level of infection in a plant species that is usually considered to be a non-host. Currently, about the only reliable criterion is the antigenic differences between the two viruses. Even here, caution must be exercised because the viruses are serologically related.

The suggestion that BWYV may be a major component of potato leafroll disease was first published in 1981 (5, 6). Duffus used aphids to transmit virus isolates from potato plants showing typical leafroll symptoms to shepherd's purse (Capsella bursa pastoris [L.] Medic.), a species that was not considered to be a host of PLRV. Further, those isolates that infected shepherd's purse showed a degree of serological reactivity in tests using BWYV antiserum.

The work by Duffus appears to establish that BWYV is a major component of the potato leafroll syndrome in North America. Isolates were recovered from potatoes affected with leafroll from widely separated geographic areas including California, Oregon, Wisconsin, Maine and British Columbia. They reacted serologically in a similar manner to BWYV isolates obtained from beets, crucifers and composites, but they differed from each other in their specific serological reactions. The logical next step was to see if leafroll from other parts of the world also contained a BWYV component. Work done on potato cultivars in Tasmania (7) confirmed that the leafroll syndrome there was essentially the same as in North America. Since strict quarantine measures had been enforced in Tasmania since the early 1930's, the authors suggested that there was probably a long term association of BWYV with potato leafroll disease. This report, together with the observations of leafroll in North American sources, led them to the suggestion that BWYV probably spread with movement of potato tubers throughout the world before the introduction of certification schemes and quarantine restrictions.

Duffus' conclusion that BWYV is widely distributed in North America is supported by Sibera and Slack (16), who examined 519 potato plants, representing 18 cultivars, originating from Wisconsin, Maine, Minnesota, Nebraska and North Dakata, using antisera specific for PLRV and BWYV in the ELISA procedure. The incidence level of these viruses was 4% for BWYV alone, 16% for PLRV alone and 65% for BWYV and PLRV. Neither virus was detected in some of the plants showing leafroll symptoms. A comparable study by Zitter et al. (19) reached similar conclusions. They found that PLRV was the dominant virus, occurring in 82 of 86 samples, with BWYV occurring in 21 of 65 samples, and that BWYV alone was found in a single sample. The infected samples were taken from the Florida winter test plots and the origin of those samples that were infected with BWYV included most of the provinces of Canada (British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, New Brunswick, Nova Scotia and Prince Edward Island).

With the impressive body of scientific evidence that has accumulated in support of the hypothesis that BWYV is a major component of the leafroll syndrome, there is a strong temptation to join the bandwagon and accept the hypothesis as fact. I for one have had difficulty with the hypothesis since it was first proposed in 1981. As more evidence has accumulated in the intervening 5 years, I have been forced to retreat somewhat in my scepticism to the point where I am prepared to admit that BWYV can infect solanaceous plants and indeed may occasionally be isolated from potato. I never have accepted the hypothesis that it is a major component of the potato leafroll syndrome. To hold such a position may appear to be close-minded, stubborn, or unable to accept new information and adjust accordingly. I therefore feel compelled to outline a case in support of the hypothesis that leafroll is essentially caused by a single virus, PLRV. In doing so, I do not wish to imply that the scientists promoting the BWYV hypothesis are careless in their experimental procedures. Rather, I feel that their biological and serological data was incomplete and may be subject to misinterpretation.

The problem with accepting Duffus' conclusions is two-fold. First is the assumption that those isolates that are aphid-transmitted from infected potato to shepherd's purse must be BWYV and not PLRV. Admittedly, PLRV is considered to have a narrower host range than BWYV but there is no *a priori* reason why it should not include shepherd's purse. Thomas (18) found that the Australian isolate of tomato yellow top virus, a strain of PLRV, had a host range that was mainly restricted to Solanaceae, though shepherd's purse was symptomlessly infected. Further, an isolate obtained from leafroll-affected potato, which produced typical leafroll symptoms in potato and a symptomless infection in shepherd's purse, reacted in gel diffusion tests with PLRV antiserum.

My second problem is with interpretation of the serological tests that were done by Duffus (5). He used a technique that involved incubating virus-antiserum mixtures, subjecting the mixture to density gradient centrifugation and analysing photometrically. A positive assay is based on the reduction or elimination of the virus peak in the scanning patterns of density gradient columns. While I can agree that a reduction of the antigen in the scanning pattern would be evidence that a virus-antiserum interaction occurred, such a test would not distinguish between a serologically related antigen and a serologically specific antigen. Since BWYV and PLRV are serologically related (8, 9), one would expect a reduction in the scanning pattern in virus-antiserum mixtures where PLRV is incubated with an antiserum prepared against BWYV. In conclusion, Duffus' data could be interpreted to show that isolates of PLRV, serologically related to BWYV, can be transmitted by aphids from potato to shepherd's purse.

The other reports (16, 19) implicating BWYV with the leafroll syndrome were based on results obtained by the ELISA technique using antisera specific for BWYV and PLRV. These reports were published in abstract form only so no details are available that would enable a reader to assess the reliability of the detection and identification of the two viruses. However, preliminary work done at Vancouver (10) showed that there may be problems in obtaining unequivocal identification of PLRV and BWYV isolates using the ELISA technique and polyclonal antisera. We found that some isolates of both PLRV and BWYV could be detected in double sandwich ELISA using homologous antisera. Further, detection was achieved when using heterologous antisera for coating provided homologous antisera were used for conjugates. With the indirect ELISA, purified BWYV was detected using PLRV antiserum but PLRV was not detected using BWYV antiserum.

Antisera prepared in rabbits often have relatively high levels of nonspecific reactions, which makes interpretation of ELISA results less than ideal. This problem can be overcome by using monoclonal antibody technology, which provides a means whereby an unlimited supply of a uniform antibody of a required specificity may be produced. With this objective in mind, Martin and Stace-Smith (12) produced some hybridoma clones that secreted antibodies specific to PLRV. These antibodies proved to be most useful in an indirect ELISA using leaf sap from PLRV-infected potato as coating and goat anti-mouse peroxidase as conjugate. They detected all of the PLRV strains that were tested and, with the exception of one isolate that was labeled BWYV, did not react with other luteoviruses. Probably, the one BWYV isolate that reacted was either mislabeled or may have been obtained from a mixed infection.

Until recently, a monoclonal antibody reacting specifically with BWYV has not been available. A project to develop such a probe at the Vancouver Research Station began in 1985 and was successfully completed in 1986 (P. Ellis, unpublished). To date, three hybridoma cell lines that appear to be highly specific to BWYV have been developed. One of these has been extensively tested, using 22 luteovirus isolates. It reacted with 16 isolates of BWYV originating from Canada, USA and Australia. It showed no cross reactivity in tests with PLRV, solanum yellows virus and subterranean clover redleaf virus, although it did show a weak reaction in tests using barley yellow dwarf virus (RPV isolate but not PAV isolate).

The availability of specific monoclonal antisera against both PLRV and BWYV has opened the possibility of a more critical examination of the role of BWYV in the potato leafroll disease. This has already begun with potato plants originating from various parts of Canada that were included in the Florida winter test plots (P. Ellis, unpublished). With the cooperation of potato seed certification officials, tubers taken from plants that were diagnosed as leafroll positive from visual examination were shipped to Vancouver, treated to break dormancy, and the sprouts were assayed for both PLRV and BWYV. Monoclonal antibodies prepared against PLRV and BWYV reacted strongly against the homologous virus but exhibited no cross reactivity when used in heterologous tests. Assays were done by the triple sandwich ELISA technique, using polyclonal rabbit antisera for coating, monoclonals as the second antibodies, and rabbit anti-mouse coupled with alkaline phosphatase as the conjugates. Tuber samples originating from Prince Edward Island (8), Nova Scotia (6), Quebec (9), Ontario (8), Manitoba (2), Alberta (2) and British Columbia (3) all tested positive for PLRV and negative for BWYV. These results indicate that BWYV is not a major component of leafroll infections in these tests and indeed may be completely absent from Canadian seed potatoes.

The possible involvement of BWYV in potato leafroll disease in other parts of the world is far from settled. In a recent publication, Barker (3) presented evidence that potato is not a host of British isolates of BWYV. He was unable to transmit BWYV to virus-free potato plants, either by itself or in association with PLRV, by _M. persicae_.

ECOLOGY AND CONTROL OF POTATO LEAFROLL VIRUS

In the previous section I have concluded that the leafroll disease is probably caused by a single virus, PLRV. The virus has a natural host range that is restricted primarily to solanaceous species, and exists as a number of biological variants that are antigenically identical or closely related.

All isolates infect potato cultivars and _Physalis floridana_ Rydb., inducing symptoms that vary from mild to severe. Some workers have designated the various isolates as mild, moderate and severe strains; others have arbitrarily divided them into four categories and referred to them as strains 1, 2, 3 and 4. Since the only difference between these strains is the intensity of symptoms induced in the host plants, it is probably preferable to refer to the range of isolates as biological variants rather than strains. The luteovirus that occurs naturally in tomato, tentatively designated tomato yellow top virus, is serologically closely related to PLRV (10, 17) and it appears reasonable to consider these as belonging to the tomato strain of PLRV.

The virus is confined essentially to potato and infection is perpetuated in tubers produced from infected plants and planted as seed or surviving overwinter in the ground and sprouting the following year as "volunteers". The virus is efficiently transmitted in a persistent manner by aphids that colonize the infected potato plants, *M. persicae* being the most important vector species. The virus is spread over long distances by windborne winged aphids and over short distances by alate or apterous aphids moving from plant to plant. Solanaceous weeds may become infected but, since these weeds are annuals, they probably play a minor role as infection sources. In fact, there is no evidence indicating that hosts other than potato act as a virus reservoir in the temperate regions (14). For this reason, one of the most important control strategies is aimed at reducing the virus sources within the potato crop.

Potato leafroll is one of the most serious diseases of potato and is responsible for high yield and quality losses in most areas of the world where potatoes are grown. In those few regions where leafroll is not of great economic importance it is of potential significance and could rapidly develop into an important disease if control measures were relaxed. The impact of the disease reflects both its effect in decreasing tuber yield and the expense and difficulty in devising effective measures of preventing its spread. Over the years a variety of control measures have been devised and a combination of these are implemented wherever potato is grown as a commercial crop.

In this paper, I shall briefly discuss those control measures that are currently being used in Canada and secondly, I shall examine control strategies that may be helpful in the future. Those measures that are being used are all aimed at reducing the incidence of the disease in those tubers that are used for seed and, while there are many aspects involved, there is only a single strategy, namely devising an effective seed potato certification system.

Seed Potato Certification

In 1914, two years before the infectious nature of potato leafroll was described, Dr. Gussow, Canada's first Dominion Botanist, initiated the Seed Potato Certification Service. This action was taken in concert with officials of the United States Department of Agriculture who were introducing a similar system in U.S.A. The basic objective of seed certification at the time was to provide the potato industry with seed potatoes that were found worthy of such certification through varietal purity and freedom from disease. From its inception, this service has made a major contribution to the potato industry, to growers of both seed potatoes and of table stock. Many refinements of methods and procedures have been introduced and continue to be introduced. In 1938, when the Plant Protection Division was organized, responsibility for the Certification Service was transferred from the Division of Botany to the Plant Protection Division. No major change occurred in Canada's seed potato certification program until 1969, with the introduction of the "Elite" seed program and the "flush-through" system. The Elite seed program required that seed eligible for certification originate from tubers or plants tested for all diseases, and limited the number of years the seed could be derived from this tested material.

With respect to control of leafroll by seed potato certification, reliance is placed on the following steps:

1. Ensure that nuclear stock is derived from PLRV-free tubers.
2. Provide an acceptable environment for nuclear seed production (greenhouse, screenhouse, selected field location).
3. Provide an acceptable environment for the propagation of each class within the certification system (select field locations where vectors are few or late in arriving; isolate seed stock from table stock).
4. Undertake field inspections as required; rogue plants with leafroll symptoms; reject plantings that exceed tolerance levels.
5. Apply insecticides as required to minimize vector activity.
6. Destroy vines or harvest crop when aphid populations reach an unacceptable level.

Some of the steps that are used for leafroll control in seed potatoes may be applicable to crops that are grown for table use or processing. In general, leafroll is not as serious in the crops that are grown for consumption rather than for use as seed because, in many cultivars late season spread would not appreciably affect yield or quality. However, particular attention must be given to leafroll control when growing cultivars that are subject to internal net necrosis. With the cultivar Russet Burbank, and to a lesser extent Green Mountain and Norgold Russet, net necrosis may be found in tubers from plants with primary, secondary or tertiary infection. The crop is not considered marketable if more than 5 percent of the tubers show symptoms of internal net necrosis.

Post-harvest Testing

With strict adherence to the control measures outlined above, experienced growers in cooperation with experienced officials usually succeed in producing a crop that meets tolerance limits for PLRV. However, detection in the field is based on visual inspection and, if vigilance is relaxed late in the growing season, considerable spread of PLRV may occur without the infection being detected until the following year when the tubers are planted. Since this is an all-too-frequent occurrence with PLRV, many seed potato certification agencies have devised a post-harvest testing procedure to monitor virus incidence.

It is a requirement of all U.S. certification programs that a winter index be performed on seed entered as foundation stock. Soon after harvest, a representative sample of tubers from each foundation block is treated to break dormancy and planted in field plots in either southern Florida or southern California. During January for Florida or February for California, the plants are evaluated for disease incidence. As a consequence of the winter index, results of the previous year's field evaluation may be either corroborated or invalidated before spring planting begins, and recommendations are provided for the foundation stock, not only with respect to disease incidence but also varietal purity and vigour. The U.S. certification programs place a high degree of importance on this winter indexing as apparent by the fact that it is a requirement for the foundation seed tag. The maximum leafroll tolerance in winter tests ranges from 0.3 to 1.0% for Foundation Grade or 0.8 to 5.0% for Certified Grade (2).

In contrast to the certification programs in the U.S.A., post-harvest testing of seed potatoes in Canada has never been part of the certification process. Despite this, the province of New Brunswick submitted seedlots to the Florida winter test as early as 1945 and other provinces joined the program in later years. In 1981, Agriculture Canada assumed responsibility for the Florida winter tests and all provinces except Newfoundland were invited to participate. In 1986, the program included the testing of 2438 seedlots with a cost to Agriculture Canada of about $180,000. However, participation in the program is voluntary and is used primarily by the grower to determine whether his crop should be sold as seed. The test has been valuable in preventing poorer seedlots being planted although post-harvest standards have not been set and regulated.

It must be emphasized that leafroll is only one of several diseases that may be detected by the grow-out test. It is also useful in detecting the mosaic viruses, spindle tuber and mycoplasmalike organisms. When disease detection is coupled with the observations that can be made on varietal purity and vigour, it would appear desirable to make such tests a requirement for seed potato certification, particularly for seed that may be shipped for export.

With respect to PLRV, a post-harvest test based on visual inspection was, until a few years ago, the only means available for determining the extent of late season infection. However, with the development of the ELISA technique and the availability of good quality antiserum against PLRV, a serological test is a practical alternative. In early trials, extracts of virus-free potato tubers gave high background readings in the standard double sandwich ELISA, with the result that PLRV detection was unreliable (15). However, nonspecific reactions can be minimized by pre-incubating the extracts at room temperature and by careful choice of the dilution of enzyme-conjugated globulin (17) or by artificially breaking dormancy (8). By modifying the standard procedure, tests on tubers from field-grown plants infected early in the season provide a true estimate of the incidence of PLRV but those on tubers from plants infected late in the season and with partially infected progenies underestimate PLRV incidence. The ELISA-PLRV test is now included in routine post-harvest testing done in Switzerland and Germany (J. McDonald, personal communication). When properly done, tuber tests are almost as reliable as other tests and PLRV incidence will only be seriously underestimated when there has been a massive invasion of the crop by viruliferous aphids late in the season. While this is possible in seed-potato growing districts if heavily infested table potato stocks are grown in the vicinity of the seed stocks, it is unlikely to occur if the seed-potato fields are properly isolated and where aphid populations are monitored.

A committee from Agriculture Canada is currently reviewing Canada's seed potato certification program design and inspection procedures in relation to those of other major seed producing countries. The objective of this review is to design an improved program which will ensure that Canadian seed potatoes are allowed access to and are competitive in all markets, both export and domestic. This committee has agreed on the desirability of eventually shifting post-harvest testing from Florida into the laboratory but it feels that replacement of the Florida tests should be delayed until a detailed evaluation is completed with acceptable results (E.M. Smith and P. Froese, personal communication). It should be noted that a laboratory test for PLRV is only one of a number of tests that require evaluation.

HOW EFFECTIVE ARE CONTROL MEASURES?

An indication of the effectiveness of the total control strategy that is employed today can be obtained by examining seed potato certification records over the past several years, with particular attention to the reasons that are given for rejecting fields that were entered for certification. The records for British Columbia vividly record the severity of the leafroll problem in the late 1950's as compared to more recent years. I have not examined the certification records from other provinces but I am assuming that a similar pattern would emerge. In British Columbia, leafroll was a major reason for rejection of fields during the period 1956-1960. The intensity of the problem during this period as compared to a recent 5 year period is summarized in Table 3.

Table 3. Rejections due to leafroll in fields entered for certification in British Columbia, 1956-1960 and 1981-1985

Year	Number of fields	Number of hectares	Percent of total	Year	Number of fields	Number of hectares	Percent of total
1956	19	27.3	22.8	1981	0	0	0
1957	27	65.5	56.4	1982	0	0	0
1958	67	232.2	79.2	1983	0	0	0
1959	125	351.1	78.2	1984	1	5.0	1.0
1960	81	261.2	68.5	1985	2	10.5	1.8

The reasons for the high incidence of leafroll were not completely understood at the time. In retrospect, it appears that there was no single factor but rather a combination of the following factors:

a. A climatic trend towards mild winters increased the survival rate of overwintering aphids.
b. The sugar beet seed industry in the Fraser Valley provided an attractive overwintering host for the green peach aphid and ensured a high vector population.

c. Inoculum sources were prevalent: some of the potato seed sources that had passed certification by visual inspection were infected with as much as 30% leafroll the following year.
d. Cultivars such as Kennebec could carry PLRV without showing visual symptoms, thus providing an inoculum source for spread to more sensitive cultivars.
e. Granular systemic insecticides were not available and aphid control with the recommended insecticides was inadequate.
f. Defoliation of potato plants to prevent late season infection was not a standard practice.

There is a danger that we may get the wrong message from the data summarized in Table 3. One might conclude from the recent records that PLRV is no longer a serious problem and, provided the recommended control strategy is followed, the incidence will remain low. Such a complacent attitude could be dangerous. While it is unlikely that the high incidence that was experienced in the 1950's will be repeated, there will almost certainly be minor leafroll problems every year and serious problems in some regions of the country. It is virtually impossible to eliminate all sources of inoculum and vector control is difficult to achieve. Fluctuations in vector populations are inevitable because (a) some seasons are more favourable than others for aphid survival and spread and (b) cyclical climatic trends will provide environmental conditions at intervals that favour high aphid populations.

Even in those regions where PLRV incidence does not exceed the tolerance level and therefore does not constitute a major reason for rejection of fields entered for certification, the virus remains in the background as a constant threat. Readings taken at the Florida trials are clear evidence of this threat. In the 1985 trials, for instance, leafroll was detected in some seedlots originating from every province (Table 4).

Table 4. Incidence of leafroll recorded in Canadian seedlots included in the Florida winter tests, 1985

Province	Samples entered	Number with leafroll	Severity <1%	Severity 1-5%	Severity >5%
P.E.I.	905	107	93	13	1
Nova Scotia	11	3	3	-	-
New Brunswick	898	78	74	4	-
Quebec	200	110	68	40	2
Ontario	112	33	20	12	1
Manitoba	60	5	4	1	-
Saskatchewan	7	1	1	-	-
Alberta	14	2	2	-	-
B.C.	136	7	6	1	-

HOPE FOR THE FUTURE

Devising a strategy for the control of potato leafroll disease is an objective of virtually every country that produces potatoes as a commercial crop. Even though a reasonably satisfactory strategy is in place in most countries, I believe most officials involved in administering potato certification programs would admit that there are serious defects and they would welcome any breakthroughs that research may provide. The major problem with the control strategy that is in place at the present time is that it requires close monitoring and quick action if there is an indication that aphid populations in seed potato fields are reaching a critical level. Such close monitoring is expensive to administer and, if it is relaxed, it may result in rejection of a crop that is excellent in all other respects. Let us look at developments over the past few years and see if they offer any hope for the future.

Improved Understanding of the Ecology of PLRV

Over the past decade there has been one major advance in the control of PLRV, namely the dramatic improvement in detection techniques. Prior to 1978, PLRV infections were detected on the basis of symptoms induced on the potato plants or on indicator plants inoculated with aphids previously fed on the suspect potato plants. Thanks to the development of the ELISA technique and the availability of high quality antisera against PLRV, we can now quickly and reliably detect PLRV infections in potato or other suspect hosts. Further, by using a modified ELISA procedure it is possible to detect the virus in individual aphids (11). This development has enabled research and extension workers to undertake extensive monitoring programs on a modest budget. Such monitoring programs will provide basic information on the ecology of PLRV and more precise control recommendations. This line of research will not result in any breakthrough but it may reduce the level of PLRV in certified and table stocks.

Breeding for Resistance

Attempts to breed modern cultivars with improved resistance to PLRV are hampered by two factors: a) genes conferring PLRV resistance are often linked with those for undesirable traits such as poor tuber shape, size and yield and b) genetic control for resistance is complex, involving more than one gene. Identification of the most resistant genotypes among the progeny of crosses between resistant and susceptible parents is therefore not straightforward. Most breeding programs concerned with PLRV resistance rely on field exposure trials in which the performance of the genotype under test is compared with that of standard cultivars. Two approaches are possible, one searching for plant virus resistance and the other for plant aphid resistance. Mndolwa et al. (13) concluded that there are good sources of PLRV resistance in *S. tuberosum* cultivars and, under field conditions that favour high numbers of viruliferous aphids, plant virus resistance may be more important for effective control of PLRV than plant aphid resistance.

Assessments based on field exposure trials provide little information on the mechanisms underlying resistance and do not allow different mechanisms to be distinguished. One feature of potato genotypes that was thought to contribute to their resistance to PLRV in the field was recently investigated in Scotland (4). Plants of a range of potato genotypes differing in rating for field resistance to PLRV were inoculated with the virus by grafting or by aphids. PLRV infected all plants and was detected by ELISA tests in the upper leaves of all genotypes. Most genotypes with high resistance ratings developed mild primary and secondary symptoms whereas those with low resistance ratings developed more pronounced symptoms. The concentrations of virions in genotypes with a high resistance level was only 1-10% of those in genotypes with low resistance levels, in samples of young or old leaf tissue. In contrast, virus concentration in vascular tissue at the heel end of tubers of plants with primary infection was similar for all of the genotypes tested. From their experiments, the authors concluded that potato varieties in which PLRV reaches only low concentrations, causes only mild symptoms and spreads slowly from plant to plant should be useful for table crops in a wide range of environments, especially in countries where the infection pressure is great or where there is no scheme for producing virus-free stocks.

In conclusion, it is evident that the traditional plant breeding approach has not met with much success in PLRV control. With the difficulty that plant breeders have had in combining desirable agronomic characteristics with PLRV resistance, it is unlikely that those cultivars that are popular in Canada today will be replaced by PLRV-resistant cultivars in the foreseeable future. However, genotypes in which the concentration of PLRV virions is low and, as a consequence, virus acquisition by vectors and plant to plant spread is slow, may be usefully exploited. For example, such a cultivar might be useful in those areas of Canada where potato growing has traditionally been a risky venture because of the high incidence of leafroll in some years.

Gene Manipulation

Advances in biology continue to be made at a striking and ever increasing rate. One of the pace setters is gene manipulation, often popularly referred to as genetic engineering. At the present state of the art, basic techniques are well established and the trend is towards applying them to solve particular problems. Some researchers feel that genetic engineering techniques provide a more rapid, more effective and perhaps a more economical alternative to established breeding methods aimed at developing cultivars resistant to plant pathogens. Is it possible that effective leafroll control could be achieved by gene manipulation? Certainly the possibility is there. Whether it can be achieved within the next few years is another question.

The recent developments of vectors for plant transformations based on the Ti plasmid of *Agrobacterium tumefaciens* has led to the expression of foreign genes in plant tissue cultures. As a logical progression of this, molecular biologists have considered the possibility of introducing foreign genes into a plant, which might prevent a virus from infecting the plant and causing severe disease symptoms. There is a recent report (1) of a chimeric gene containing a cloned cDNA of the coat protein of tobacco mosaic virus being introduced into cells on a Ti plasmid of A. tumefaciens. Plants regenerated from transformed cells expressed TMV mRNA and coat protein as a nuclear trait. Some of the seedlings from self-fertilized transgenic plants expressed the coat protein gene and failed to develop symptoms when inoculated with TMV. These results indicated that plants can be genetically transformed for resistance to virus disease development.

By using similar genetic engineering techniques, a potato plant might be genetically transformed for resistance to leafroll. The major advantage of this approach as opposed to breeding for resistance is that the existing cultivars that are in high demand by the industry (e.g. Russet Burbank) would not be replaced, but merely transformed by the insertion of a small segment of the viral RNA. In theory, this could be done in such a way as to retain the genetic integrity of the cultivar yet incorporate a degree of resistance into the plant genome. If the viral coat genome could be incorporated into the potato genome, PLRV coat protein might interfere with viral replication, thereby delaying or preventing the expression of symptoms.

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ROLE OF PLANT RESISTANCE IN CONTROL OF THE POTATO VIRUSES

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ABSTRACT

The common potato viruses could be eliminated from the Atlantic Canada seed-growing areas if available resistance characters were utilized. Of the aphid-borne viruses, we have extreme resistance to viruses A, S, and Y, and adequate resistance to the leaf roll virus. The contact-transmitted virus X (for which we also have extreme resistance) and the spindle tuber viroid can be controlled by means of rotational seed certification. None of these viruses is endemic to the natural vegetation of the region. Thus, reputed resistance-breaking strains and other 'exotic' viruses can be introduced only through our own carelessness. Actually, the resistance characters have already been assembled, in various combinations, in good quality cultivars. With these as key parents, our breeders face the challenge to produce replacements for some popular, but susceptible, commercial varieties.

RESUME

Les virus communs de la pomme de terre pourraient etre elimines des zones de production de semence dans l'Atlantique si les caracteres de resistance disponibles etaient utilises. En ce qui concerne les virus transmis par les pucerons, nous possedons des elements de resistance elevee aux virus A, S, et Y ainsi qu'une resistance adequate a l'enroulement. Le virus X, transmis par contact, (et pour lequel nous avons des elements de resistance eleve) et le viroide de la filosite peuvent etre controles au moyen du systeme rotationnel de certification de la semence. Ces virus ne sont pas endemiques a la vegetation naturelle de la region. En consequence, les souches de virus qui pourraient briser la resistance et les virus "exotiques" ne peuvent etre introduits que par notre manque de prudence. En realite, les caracteres produisant la resistance ont deja ete assembles, en differentes combinaisons, dans des varietes de bonne qualite. Nos geneticiens ont maintenant devant eux le defi de developper, a partir de celles-ci, des varietes de remplacement pour les varietes commerciales populaires mais susceptibles.

INTRODUCTION

Ten years ago, I wrote a chapter on the subject I have today, "Resistance to viruses in potato". I referred to the potato-infecting viruses as a 'Cosy little club' (1). Since that time, the membership has grown a bit and the importance of several has shifted significantly. There has also been some progress with regard to resistance.

There are several categories of membership in the so-called club:

(I) Viruses commonly found in the Canadian crop; more particularly that of the seed-growing areas of the Atlantic region:

Potato leaf roll virus (PLRV)

Potato virus Y (PVY)

Potato virus A (PVA)

Potato virus S (PVS)

Potato virus X (PVX)

Potato spindle tuber viroid (PSTV)

(II) Viruses common in potato in some other countries, but apparently not so in Canada. Amongst others, these include:

Potato virus M

Potato aucuba mosaic virus

Potato yellow dwarf virus

Tobacco necrosis virus

Tobacco rattle virus

(III) A group of 'exotic viruses'--perhaps 8 to 10 if we include special strains of some of the common viruses--which are largely confined to the areas of South America whence the potato originated.

There is a fourth group of plant viruses--really not potato viruses--which sporadically invade the crop. These include two of the most widespread plant viruses, cucumber mosaic virus and tobacco mosaic virus. They are resisted and rejected by the potato plant, as are many other plant viruses. These viruses are, nevertheless, part of our story, for their treatment by the potato illustrates one of the cardinal principles of plant pathology. Resistance is the rule and susceptibility is the exception. We can be thankful for this because these viruses number more than a hundred. If it were otherwise, the entire plant kingdom, let alone the potato would be hard put to survive.

I am relieved, too, that we do not have problems with the second group of viruses, as several of them are difficult to control. They and the Group 3 'exotics' should be subject of studies on quarantine. And I will sound a note of warning to those who advocate growing potatoes from true seed. Several of the South American group, like the spindle tuber viroid, are seed-borne.

I plan to speak further only of Group 1 viruses--those of immediate concern. But first, we need to consider some background; the types of resistance and the means of detecting them.

TYPES OF RESISTANCE

We find several apparently different categories of resistance to viruses in the potato. But when we examine them critically, they are seen as varying degrees of what is called general resistance, either alone, or in combination with a hypersensitive response by the plant:

(a) General resistance: (also termed: field, polygenic, non-specific, minor-gene, or horizontal resistance). This supposedly may include anything that inhibits infection, multiplication of the virus, or transport to the tubers. There is evidence in several instances that restricted virus multiplication is the major effect. In most cases this resistance appears to be multigenic, but there are several where high field resistance is controlled by a single gene.

(b) Hypersensitive resistance: (also: intolerance, field immunity; monogenic, specific, major-gene, or vertical resistance). This type of resistance is associated with death of the individual protoplasts as a result of infection. It appears to depend on support from a general type of resistance for effectiveness. Spread of the virus may be halted at the cell level, within a localized lesion, or by leaf-abscission. But it may continue to spread throughout the plant, doing such damage that the current or second generation plant is destroyed without producing viable tubers. Unless infection pressure from outside sources is extremely high--a condition rare in Canadian seed-growing areas--infection sources within the crop die off faster than new infections occur. Van der Planck (9) has referred to this latter effect as 'population-immunity', as opposed to plant resistance.

(c) Mature plant resistance: As leaves on the potato plant mature, they become more resistant to infection with all of the viruses involved here. The onset of this type of resistance has been correlated with a rapid decrease in ribosome and RNA content of the leaves. Beyond a certain stage, which varies with the virus and the cultivar, virus is prevented from reaching the tubers.

(IV) Immunity: What we have regarded as immunity to PVA, PVY, and PVX is actually extreme resistance--slow initial development of the virus, coupled with hypersensitive response by the plant. I know of no absolute immunity or null-reaction by the potato to any of these viruses.

METHODS OF TESTING FOR RESISTANCE

There are two essential steps: (a) Inoculation. (b) Observation or test to determine if systemic infection has occurred. The observation may also reveal the occurrence of a specific resistance reaction. Practically every method by means of which viruses can be transmitted or detected has been used. A summary follows:

Inoculation

Field exposure trials, with or without infector plants.

Artifical inoculation.
  Aphids fed on infector plant, transferred to healthy.
  Healthy plants or tubers caged with aphids on infected.
  Mechanical inoculation by rubbing or spraying.
  Grafting healthy plants or tubers with infected.

Observation or detection:

Replant tubers, observe symptoms in field or greenhouse; spot-test for virus by means of differential host or serology.
Serological test on original plants, tubers, or replants for presence or quantity of virus.
Observe potato plants for localized lesions or 'top-necrosis' reactions, denoting specific resistance.

RESISTANCE TO VIRUSES TRANSMITTED BY APHIDS

Potato leafroll virus (PLRV)

This is a persistent-type virus spread largely by the potato-colonizing aphid, Myzus persicae (Sulzer). The virus is widespread in warmer climates, but the Maine-New Brunswick seed growing area is on the northern fringe of its range. We have epidemic spread only during warmer phases of the climate (i.e. 1906-1912, 1937-1945, 1972-1976) (2). Between epidemics, control can be affected by encouraging early crop maturity (mature plant resistance). If this is done, top-kill can be used to control size of the tubers.

Replacement of the susceptible processing cultivar Russet Burbank with a moderately resistant cultivar free from 'net necrosis' (i.e., resistance equivalent to Katahdin--but with high processing quality) would greatly lessen the effect of the periodic epidemics. We have resistance in our breeding program sufficient to eliminate PLRV from our prime seed-growing areas.

The resistance is of the general, multi-genic type. Scottish workers have shown that in many resistant cultivars, development of the virus is restricted (5). Some are almost symptomless carriers when infected--a potential problem for seed growers. Other cultivars, including a number of Fredericton seedlings combine good symptom development with high resistance.

Potato viruses Y and A (PVY, PVA)

These non-persistent-type viruses are also spread efficiently by *M. persicae*, but more so during the early flights than is PLRV. The viruses are spread, too, by a number of aphids which merely visit potatoes in search of a feeding site. Some of these other aphids--unlike *M. persicae*--are well adapted to our northern climate. Consequently, they appear earlier in the season. PVY has been more consistently present in our seed crop than has PLRV, and has fluctuated on a shorter period.

The United States Department of Agriculture found PVA widespread when they started a breeding trial at Presque Isle, Maine about 1919. Early selections and crosses led to Katahdin, which possessed a general type resistance, and was practically field-immune to PVA. No immunity could be found for PVY but Katahdin was later shown to be highly resistant.

A cluster-analysis of data from our own PVY-resistance trials has split 40 cultivars into 2 susceptible and 3 resistance categories--most of the latter with Katahdin lineage. Performance of the resistant cultivars as compared with that of the susceptibles in the New Brunswick Florida Test indicates that exclusive use of the two most resistant categories would eliminate PVY (and PVA) from this area (3).

There are also quality seedlings in the Fredericton breeding program bearing genes for immunity to PVY--from both *Solanum stoloniferum* and *S. tuberosum* subsp *andigena* sources. Both are inherited as dominants.

Potato virus S (PVS)

Aphid-transmitted strains of this virus appear to be be more widespread than had been supposed. Perhaps this is because the introduction of virus-free stocks have permitted greater spread and thus selection. PVS is also transmitted in a non-persistent fashion; and its epidemiology resembles that of PVA and PVY.

We had field-immunity to PVS in the cultivar Saco less than 5 years after this virus was discovered. This type of resistance, inherited as a recessive, is also present in the Fredericton cultivar, Jemseg. Hypersensitive type resistance to PVS, inherited as a dominant, has been found in *Solanum tuberosum* subsp *andigena* and in *S. megistacrolobum*. We have recently selected some healthy seedlings with the N_s gene from amongst a lot of seed that was partially contaminated with PSTV. Thus, we have parents with both dominant and recessive types of resistance to PVS.

RESISTANCE TO MECHANICALLY TRANSMITTED VIRUS AND VIROID

The other two members of the 'potato virus club' that I mention have been dealt with last--deliberately. They are in some danger of losing their membership at least to the New Brunswick Chapter.

Potato virus X (PVX)

There have been reports that PVX is transmitted by several insects--but little in the way of confirmation. We have both hypersensitive-type resistance and immunity. Resistance-breaking strains have been reported for both (6)--but there appears to be little danger that either will become widespread unless we are extremely careless.

The reason I think PVX could disappear is not due to resistance, but to the success of the virus-free program. It has not been completely effective as yet. But there seems to be no reason why the rotational-seed certification plan (or flush-through system as some call it) will not eliminate this virus, given complete cooperation by the growers.

I have suggested to the breeders that they develop a number of cultivars for the home garden which carry immunity to PVX and PVY, plus resistance to PLRV. We could be rid of a troublesome reservoir of these viruses whilst gaining some experience with quality development.

Potato spindle tuber viroid (PSTV)

PSTV is apparently spread less readily than PVX--else it would have become much more widespread than was actually the case. The seed-rotation plan has already eliminated virtually all detectable PSTV from the New Brunswick seed crop (8).

Since PSTV is seed-borne, it remains as a potential hazard to the breeders. There is some resistance to be found in wild species--and I have found some mature-plant resistance. However, I rate this as a low priority.

CONCLUSION

We have resistance with the potential to eliminate these viruses in many areas of Canada. Actually, we are well on our way, for much of the resistance is carried in reasonably good quality varieties and seedlings--be it chipping, french fry, or table (3,4).

If plant resistances were fully utilized in control of the potato viruses, the use of pesticides could be reduced drastically. Moreover, unlike resistance to the more adaptable fungi, resistance to viruses is relatively stable. We can trace resistance of PVX through Epicure (1897) to Patterson's Victoria (1856); and resistance to PVA through Irish Cobbler and Early Rose (1867) to Garnet Chili (1852) (7). The resistance is as strong against the viruses prevalent today as it likely ever was.

Were it any other crop with a troublesome group of diseases, the resistance would straight-away be put to use.

But this is the common potato.

There is still the formidable task of displacing some favorite cultivars such as Russet Burbank and Pontiac. It would take a real commitment from the breeders--so I conclude by issuing the challenge.

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COLORADO POTATO BEETLE CONTROL: ECOLOGY AND MANAGEMENT

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ABSTRACT

The Colorado potato beetle, Leptinotarsa decemlineata (Say), has one generation in most parts of Canada and two generations in extreme southern areas. The winter is spent as an adult in the soil. In spring, adults walk or fly to potato plants where eggs are laid on the foliage, larvae hatch and are normally sedentary and feed on the upper leaves of the plant. After pupation in the soil, adults also feed on the foliage before either diapausing for winter, or ovipositing. Colorado potato beetle uses chemical cues to find plants. Foliage chemistry and glandular trichomes on the leaves affect the insect's survival and performance. In the absence of insecticide use, beetle numbers are principally affected by starvation. Natural enemies have little effect. Colorado potato beetle is very adaptable and has strains which are specialised for different climates, or different host plants, or have become resistant to a wide range of insecticides.

Insecticides are targeted against Colorado potato beetle in most Canadian provinces east of Saskatchewan. Granular applications at seeding have recently become less popular; growers are switching to foliar applications. Resistance to currently used insecticides is found in several places in eastern Canada. Rotation is practised, especially in the prairie provinces, and results in most Colorado potato beetles being concentrated at field margins, where they could be controlled by spot insecticide treatments. Biological control and the breeding of resistant host plants are areas of active research in North America. Economic injury levels appear to be much lower than currently used values, and there is little prospect that their implementation will reduce insecticide use, unless spot treatments are used.

It is recommended that an integrated pest management system be implemented, to avoid the possibility of resistance to insecticides leaving no economic control methods for Colorado potato beetle. Initially this would use resistance management techniques, economic thresholds, and rotation. Studies of the economics of rotation, and the use of economic incentives for growers to adopt the scheme are advocated. Efforts should continue to add more control tactics to the integrated management scheme, for example resistant potato varieties and biological control. It is emphasized that, given the adaptability of Colorado potato beetle, it will be necessary to use strategies of managing resistance to all control tactics where that is possible, and that new control measures may continually be needed to keep pace with the evolving insect. Such an integrated pest management scheme appears to be compatible with control of several other pests, and should form part of an integrated scheme for potato management.

RÉSUMÉ

Le doryphore de la pomme de terre, Leptinotarsa decemlineata (Say), a une seule génération par année dans l'ensemble du Canada et deux générations dans les régions le plus au Sud. L'hiver se passe au stade adulte dans le sol. Au printemps les adultes émergent, marchent ou volent vers les plants de pomme de terre où ils pondent leurs oeufs sur le feuillage, les larves éclosent et se nourrissent sur les feuilles supérieures du plant. Après la pupaison, au sol, les adultes se nourrissent aussi sur le feuillage avant d'entrer en diapause pour l'hiver où de pondre des oeufs. Le doryphore de la pomme de terre utilise des messages chimiques pour localiser les plantes. La chimie du feuillage et les trichomes glandulaires sur les feuilles affectent la survie et la performance de l'insecte. Si les insecticides ne sont pas utilisés, l'abondance du doryphore est contrôlée principalement par l'abondance de nourriture. Les ennemis naturels ont peu d'effet. Le doryphore de la pomme de terre est très adaptable. Certaines souches sont spécialisées pour differents climats, ou pour différentes plantes hôtes, ou sont devenues résistantes à une grande variete d'insecticides.

Les insecticides sont utilisés contre le doryphore de la pomme de terre dans la plupart des provinces canadiennes à l'Est de la Saskatchewan. Les applications granulaires au moment de la mise en terre sont récemment devenues moins populaires; les producteurs préfèrent de plus en plus les applications foliaires. La resistance aux insecticides recommandés est présente dans plusieurs régions de l'Est du Canada. La rotation des champs est pratique courante, surtout dans les Prairies, causant la concentration des doryphores en bordure des champs où ils pourraient être controlés par des applications insecticides localisées. Le contrôle biologique et le développement de variétiés résistantes sont des domaines de recherche active en Amérique du Nord. Les seuils économiques de traitement semblent beaucoup plus bas que ceux utilisés présentement, sauf lorsque les traitements localisés sont utilises.

Un système de régie intégrée se doit d'être mis en place pour éviter la possibilité de résistance aux insecticides, ce qui pourrait éliminer toutes les méthodes de contrôle économiques disponibles. Initialement cette régie devrait utiliser les techniques de régie de la résistance, les seuils économiques et la rotation. Des études de l'aspect financier de la rotation, et l'utilisation de stimulants économiques pour favoriser son adoption par les producteurs sont suggérés. Les efforts devraient se poursuivre pour ajouter d'autres stratégies de contrôle à cette régie integrée, par exemple les variétés de pomme de terre résistantes et la lutte biologique. Considérant l'adaptibilité du doryphore de la pomme de terre, il sera nécessaire de considérer les techniques de régie de la résistance pour chaque méthode de contrôle si possible. De nouvelles methodes de contrôle seront peut-être toujours requises pour contrecarrer l'évolution de l'insecte. Un tel système de lutte intégrée semble compatible avec le contrôle de plusieurs autres parasites et devrait faire partie d'un schéma intégré pour la régie de la pomme de terre.

INTRODUCTION

The Colorado potato beetle, Leptinotarsa decemlineata (Say), is thought to have originated in Mexico where it fed on buffalobur, Solanum rostratum Dunal, (68). It was first reported as a pest of potato, S. tuberosum L., in 1859 in Nebraska (96) and has since spread to all the major potato growing regions of the world with the exception of the United Kingdom (45). Colorado potato beetle was first reported in Canada in south western Ontario in 1870 (6), and its subsequent spread was documented by Gibson et al. (31). Currently, it occurs in all provinces with the exception of Newfoundland and Labrador (3, K.Proudfoot, personal communication).

Colorado potato beetle has been the subject of extensive research throughout this century, and a number of recent symposia or reviews have been devoted in whole, or in part, to it (e.g. 27,58,75). Rather than duplicate this extensive body of recent literature, the current work will provide an overview of the biology and methods of control of Colorado potato beetle, and examine current control practices and future prospects for integrated pest management of Colorado potato beetle in Canada.

ECOLOGY OF THE COLORADO POTATO BEETLE

Life cycle

The life cycle in temperate regions is shown in Figure 1. Colorado potato beetles overwinter in the adult stage in the soil at depths of up to 43 cm in loose soil, but much closer to the surface in heavy soils; the site is often close to the final host plant of the season (31). In spring, beetles emerge in response to increasing temperatures. In Canada, beetles generally first appear in the last week of May or in early June (31). Beetles seek host plants and then the females lay eggs in masses on the leaves. Each egg mass contains about 30 eggs (31). Oviposition continues for several weeks during which females may move from older to younger plants (10).

Like the adults, larvae feed mostly on the leaves of their host plant. There are four larval instars and, except when larvae are moulting, feeding is almost continuous; usually, larvae remain near the top of the plant (31). Larvae normally do not leave the plant unless food becomes short, however they may transfer from one plant to another if the foliage intermingles (31, Morris and Holliday unpublished). After completion of feeding, larvae burrow into the soil and pupate and, 1 - 2 weeks later, adult beetles emerge (31).

In Canada, adults emerging from pupation may either feed for a while and then enter overwintering diapause, or they may immediately give rise to a second generation (Figure 1.)(31). The factors which can induce diapause are poor host plant quality and short photoperiod. Low temperatures also favour diapause induction (20). Table 1 summarizes information obtained from various sources on the number of generations of Colorado potato beetle in each province. In areas where one generation normally occurs, there may occasionally be a full or partial second generation; this usually is very late in the season and does not have a significant impact on potato yields. A second generation normally occurs in southern Ontario and southern-most Quebec. Sources differ on the incidence of a second generation in Nova Scotia. It is possible that, because of the variable maritime climate, a prolonged and poorly synchronized single generation occurs and is interpreted as two generations.

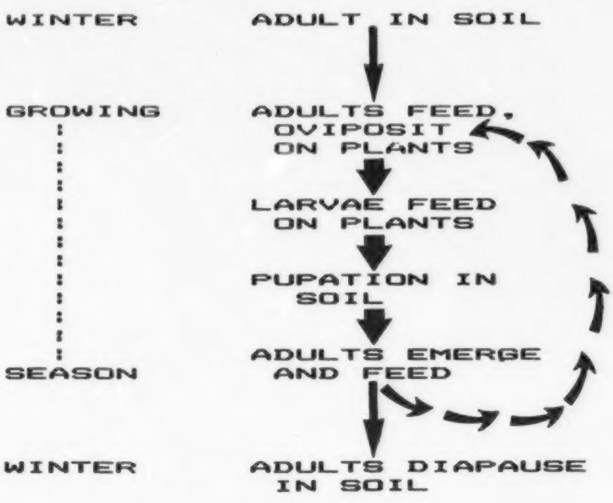

Figure 1. Life cycle of the Colorado potato beetle in Canada.

Host plant finding and suitability

Colorado potato beetle larvae seldom move far unless food is short (31, Morris and Holliday, unpublished). Thus, except at high densities, the distribution of the larvae in a field is largely determined by the pattern of oviposition. Hurst (50) has reviewed the literature on movement of overwintered beetles to host plants before oviposition. The general pattern is that when suitable hosts are close to the overwintering site, adults walk to them; where this is not so, adults fly. Walking adults are impeded by dense vegetation (69) and seldom penetrate far into a potato field (98). Beetles are weak flyers and require warm weather for flight; flights before feeding are short, while longer flights may follow feeding (50). Direction of flight has been reported to be upwind at low wind speeds (98), but mark-release studies indicate that there are preferred compass directions of movement which do not appear to be responses to host-plant distribution, wind direction, or local conditions (69, Morris and Holliday, unpublished).

A consequence of these behaviour patterns is that, when potatoes are planted following a non-host crop in a rotation but close to previously infested potato fields, the density of Colorado potato beetle larvae is very high at the edge of the field but much less so in the middle of the field. In a Czechoslovakian study, few beetles penetrated more than 120 m into a field adjacent to a previous potato field; when fields were 300 - 800 m distant from previous fields, beetles penetrated 360 m into the fields but densities were much lower (79). It is likely that adults walked to the adjacent field but flew to the more distant fields. In Manitoba, where temperatures during the oviposition period are often below the 25°C threshold (53) for sustained flight, larvae are seldom found more than 50 m from the field edge; exceptions are usually associated with uneven crop emergence (Morris and Holliday, unpublished). In New Jersey, edge effects also occur in rotated fields but, in non-rotated fields, there is no edge effect, densities of larvae are higher, and damage begins earlier (59).

Selection of host plants appears to be largely by chemosensory means. Potato spacing has no effect upon colonization, but when potatoes are interspersed with non-host plants the number of colonizing beetles is reduced (4,10). In spring, large potato plants are more attractive to Colorado potato beetle than are small plants (31). However, some adults transfer from large early-emerged plants to later smaller plants; adults feeding on smaller later plants are more fecund than those feeding on early plants (10). Both larvae and hungry, walking adults respond to odours from solanaceous foliage by walking upwind. The compounds which induce this behaviour have been termed the green leaf volatiles (94,95). But these compounds are not restricted to acceptable host plants and it is not known how the acceptability of plants is assessed (65). The host-plant range of Colorado potato beetles is largely restricted to the Solanaceae, a common feature of which is the presence of glycoalkaloids. It has often been suggested that these compounds play a role in host plant selection (e.g. 15), but it has not been possible to isolate a specialized chemoreceptor which responds to *Solanum* glycoalkaloids (67).

Among the Solanaceae, Colorado potato beetles tend to perform best on those with low foliar concentrations of total glycoalkaloids (21). In addition to the effect of total glycoalkaloids, specific glycoalkaloids such as leptines and tomatine are deleterious (86). Glandular trichomes also affect host plant suitability: high densities deter oviposition and reduce larval survival (17), adult weight and fecundity (21) (See Pelletier and King, these proceedings).

The performance of Colorado potato beetle on its host plant differs between populations (46) and is affected by temperature (34), the presence of leafroll virus (14), nitrogen fertilization of the plant (52), and the host plant of previous generations (35). Beetles may respond to changes in plant defences by entering diapause: for example, on *S. dulcamara* L., glycoalkaloids rise throughout the growing season and beetles complete an early season generation, then diapause; on *S. tuberosum* in the same area, glycoalkaloids do not increase and there is a second generation (39).

Population dynamics

Colorado potato beetles have a clumped distribution on plants (36), which may be described by a negative binomial distribution (23), Taylor's power law relationship (36,61), or by Iwao's patchiness regression (63). Any of these mathematical relationships could be used to develop a sequential sampling plan (e.g. 63). The degree of aggregation tends to be greatest for early instar larvae (36,63) and to decline through the larval instars. This is probably because the aggregation results from the habit of laying eggs in masses and this effect wanes as larvae move from plant to plant.

The most intensive study of the population dynamics of Colorado potato beetle is for isolated unsprayed potato plots in the Ottawa area (37). The most significant factor affecting populations is food shortage which results in starvation of the larvae and emigration of adults; in some years, overwintering mortality is high (up to 70% of adults entering hibernation). The only natural enemy of importance is a parasitic tachinid fly, Doryphorophaga doryphorae (Riley) (Diptera:Tachinidae). In Ottawa, this parasitoid must migrate from the south each spring and so the mortality it inflicts does not respond to density of Colorado potato beetles. The factor which both regulates and causes changes in the population of beetles is adult emigration, which has an overcompensating density dependent effect, and so causes oscillations in populations rather than stability. Analysis of life tables from 24 field studies of insects indicated that the population dynamics of Colorado potato beetle are the least stable, showing a tendency to limit cycles with two points, whereas all the others tend to converge to a single stable point (44).

Harcourt's study (37) may not be applicable in detail to all Canadian populations of Colorado potato beetle; for example, overwintering mortality and egg eating by newly-hatched larvae may be more important in some areas (31). However, it appears to be generally correct that, in the northern United States and Canada, the population dynamics are little influenced by natural enemies; certainly this is true in Washington state (88,89). Because of the absence of important natural enemies, and because food shortage is not relevant in commercial potato fields with insect control, predictive models of populations, based upon early season density estimates, may be relatively easy to develop. Logan (61) has already developed a simple model of this type for the purpose of predicting yield loss, however, such models might also be useful for assessing the effectiveness of different control strategies.

Adaptability

In less than 200 years, Colorado potato beetle has spread from its presumed Mexican centre of origin (68) to almost all the potato growing areas of North America and Europe. The enormous adaptability of the Colorado potato beetle is one of the major reasons for its successful colonisation of areas which span 45° of latitude (48) and have climates ranging from arid subtropical to maritime north temperate. Colorado potato beetles in southern Mexico do not undergo a winter diapause, but diapause during periods of host plant scarcity which normally occur during spring and summer droughts. In such areas, beetles are insensitive to photoperiodic cues and diapause takes place above ground and is terminated by reappearance of moisture and host plants (48). This pattern occurs as far north as Texas, but north of this, beetles respond not only to host plant quality, but also to diminishing photoperiod in fall. The ensuing winter diapause takes place in the soil; in different regions there are different critical photoperiods for diapause induction and these are genetically determined (47). There may also be a summer pupal aestivation in these regions (30). In extreme northern areas, adults may enter winter diapause and remain in diapause throughout two winters (31). A similar range of seasonal adaptations has been observed in Europe (20,92).

In North America, Colorado potato beetles exhibit genetically determined morphs which are adapted to particular host plants (46). There is further evidence of great genetic diversity from studies of enzyme polymorphism (51), cytogenetic studies (49), and studies of colour morphs (7,9). Hsiao (48) emphasized the importance for managing the pest of knowledge about the diversity and dynamic nature of its genetic system. He concluded that recent population increases, extension of host ranges and the development of resistance to all major groups of insecticides (13,28,29) are symptoms of the adaptability of that system.

CONTROLLING THE COLORADO POTATO BEETLE

Control of Colorado potato beetle has been recently reviewed (25,30). The following is a review of the current status of practical control and research into control measures with, where feasible, a Canadian perspective. Some areas of control will receive relatively little attention as they are to be treated elsewhere in this symposium. In order to gather information on the current status of Colorado potato beetle in Canada, a letter requesting information was sent to extension workers and research personnel in each province. In addition, published information was perused. Table 1 is a summary of the information obtained.

Importance of Colorado potato beetle in Canada.

Colorado potato beetles are not the only insects to afflict potatoes in Canada and so the importance of Colorado potato beetle cannot be considered alone. For example, in the three western-most provinces, control measures for wireworms, flea beetles or aphids reduce Colorado potato beetle populations; so specific control measures against Colorado potato beetle are seldom made, and the insect is regarded as of minor importance. A similar situation is found in Nova Scotia.

Colorado potato beetle tends to undergo periods of above average abundance which may persist for several years before the outbreak subsides. Episodes of high abundance may be fairly local, for example, Essex county in southwestern Ontario had extremely high populations 10 years ago but now densities have subsided, however, in neighbouring Kent county densities are currently extremely high (R.E.Pitblado, personal

Table 1. Summary of the current status of Colorado potato beetle and its control in Canada

	BC	Alberta	Saskatchewan	Manitoba	Ontario	Quebec	New Brunswick	Nova Scotia	Prince Edward Island	Newfoundland
1. How important is CPB relative to other pests?	Less than wireworms, tuber flea beetles, aphids	Less than wireworms, flea beetles	Less than wireworms flea beetles.	Most important	Most important	Most important	Major pest	Minor importance	Major pest	Absent
2. Is the CPB currently more or less abundant than usual?	?	?	Average to less abundant	Average	Average, declining from a peak in some areas, abundant in others.	Variable, abundant in some areas.	More abundant	More abundant	Average	-
3. How many generations are there per year on the crop?	1	1	1	1	1-2	1-2	1	1-2	1 sometimes a partial second	-
4. Typical control program	Controls for other pests obviate need	Controls for other pests obviate need.	Rotation and granular insecticides for wireworm control. Spot foliar sprays for CPB.	Rotation, 1-2 foliar sprays/ year.	20-75% use granular insecticides + ca2 foliar sprays. Others use 3-6 foliar sprays.	Granular insecticides or 1-4 foliar sprays	Granular insecticides 1-2 foliar sprays	Controls for other pests obviate need.	40-50% use granular insecticides. Remainder use foliar sprays.	-
5. Is there evidence of resistance to currently used pesticides in CPB?	No	No	No	No	Yes	Yes	Yes	No	Weak evidence	-
6. Initiatives in IPM for potato insects	Research in progress	None	None	Research in progress.	Research in progress. Commercial monitoring recently ceased.	Research in progress.	Research in progress.	None	None	-
Area grown (ha)	3510	6729	1010	16558	15829	17172	21769	1545	25851	396

Sources of information: Literature cited 1, 3, 16, 33, 72, 84, 85; Personal communications from: G. Boiteau, W. Charnetski, R-M. Duchesne, B.D. Fraser, T. Haliburton, G. Mailloux, C. Peters, R.E. Pitblado, K.G. Proudfoot, A.T. Raad, M.K. Sears, H.B. Specht, S. Squire, G. Stone, L.S. Thompson, S.A. Turnbull.

communication). In contrast, there have been wide-spread high population densities in New Brunswick throughout the 1980's.

Chemical control

CURRENT PRACTICES. The major method of controlling Colorado potato beetle is with chemical insecticides. Two approaches to this are common. Granular systemic insecticides may be applied at planting, or foliar insecticides may be applied when larvae or adults are seen on the foliage. Granular insecticides have the advantage that they provide control from plant emergence to mid season of most early season foliar and soil pests. But they are relatively expensive, may leave residues in the crop and the environment, and must be applied before insect populations can be assessed. The latter may lead to unnecessary or routine applications which favour development of pesticide resistance (See Martel, these proceedings). Foliar insecticides are much less persistent and are cheaper, they can be applied following determination that the economic threshold has been exceeded, and spot treatments of areas of high Colorado potato beetle density are possible. Foliar insecticides are often applied with fungicide treatments to reduce application costs; if ground application equipment is used, this also avoids additional soil compaction.

Chemical controls aimed specifically at Colorado potato beetle are used in all provinces east of Saskatchewan with the exception of Nova Scotia and Newfoundland, and typical control measures for each province are summarized in Table 1. In most regions the use of granular insecticides is waning. This is probably a result of the disadvantages outlined above, but possibly also because of a switch to synthetic pyrethroids which are not suitable for use in soil. With the exception of Atlantic Canada, all recommended insecticides belong to the major insecticide groups: organochlorine, organophosphorus, carbamate and synthetic pyrethroid compounds. In Atlantic Canada the top-killer dinoseb (2-sec-butyl-4,6-dinitrophenol) is recommended as a means of killing not only tops but also Colorado potato beetle adults late in the season (3,12).

Resistance to insecticides by Colorado potato beetle is less of a problem in Canada (See Martel, these proceedings) than in the northeastern United States where there are many locations in which no registered insecticide provides effective control (25). In regions where resistance is known to occur, extension literature recommends that insecticides be rotated (3). In Ontario the recommendation is that successive insecticides be from different groups (72), and this may be more effective in managing resistance than rotating among chemicals of the same group.

FUTURE PROSPECTS. There is little prospect that, in the near future, alternatives to chemical control will be effective enough to allow discontinuation of insecticide use. Continuation of economic and safe use of insecticides will depend upon having enough suitable materials available to keep pace with resistance, or in managing resistance so that the available materials provide an adequate armoury.

The current extreme caution about pesticides and their side effects is not conducive to rapid development of new compounds with new modes of action. In the last 45 years, only four major groups of insecticides, with three modes of action between them, have become widely used. Cross resistance by Colorado potato beetle within these groups is common, and cross resistance between groups is not unknown (28). Currently, there are relatively few materials with novel modes of action under test in Canada. Trials of insect growth regulators are in progress in Canada (5, C.Dobson, personal communication) and elsewhere (e.g. 2,64,90,93). In Ontario, trials of fungicides having synergistic properties with insecticides have shown some promise (74).

Instead of developing new materials, it may be possible to overcome the enhanced detoxification mechanism of resistance by using synergists to block biochemical pathways which break down currently used insecticides. Piperonyl butoxide (5-{2-(2-butoxyethoxy)bethoxymethyl}-6-propyl-1,3-benzodioxole) and other synergists for this purpose have not enhanced the performance of synthetic pyrethroids against resistant strains of Colorado potato beetle (60). This suggests that enhanced detoxification is not the mechanism of resistance to pyrethroids. Synergists might be effective against carbofuran resistance of the type described by Harris and Svec (43), because this is thought to be the result of enhanced detoxification.

The above developments do not indicate that the supply of insecticides will keep pace with the rate of resistance development in Colorado potato beetle. So in addition to the search for new materials, it would be wise to reduce the rate at which current materials become useless because of resistance. This is termed resistance management. One approach is to reduce the selective pressure which is responsible for increasing the frequency of resistant genes in a population, by minimising the number of insecticide applications. This may be done by the replacement of "spray calendar" strategies with the use of economic thresholds. Additionally, alternative controls [e.g. crop rotation (59), biological controls (77), or antifeedants (40,41,87)] may be integrated with the insecticide program. These added controls have the effect of reducing populations so that fewer insecticide applications are necessary, and also applying selection pressures which may conflict with those resulting from insecticide use. The idea of using conflicting selection pressures is also behind the practice of rotating among groups of insecticides. Simulation studies (55,62) indicate that a reduction in the rate of build-up of resistance can be expected by the rotation technique, but that applying mixtures of insecticides of different groups will have a much greater effect on the rate of selection. For maximum effectiveness of techniques dependent upon applying conflicting selection pressures, it is necessary that the affected genetic loci be linked and that genetic recombination be minimal (62).

Another approach to resistance management is to attempt to retain or augment susceptible genes within the population. This can be done by treating only high density populations, such as by adhering rigorously to an economic threshold decision rule, or by spot treatment. It is important to protect non-economic populations from insecticides, as these will provide a pool of susceptible genes. Insecticide applications to economic populations should be at a dose sufficient to kill the heterozygote carriers of the resistant gene (62). Heterozygotes are frequently partly resistant and, in the early stages of resistance build-up, the majority of resistant genes are carried by heterozygotes. Augmentation of susceptible genes by release of susceptible individuals has been proposed for resistance management in mosquitoes (19); however, this may be difficult to apply to Colorado potato beetle because of the absence of a satisfactory artificial diet for rearing large numbers of beetles (11).

Some of the most effective techniques of resistance management are inconvenient or take away the farmer's freedom to choose the cheapest or otherwise most attractive insecticide. Further, because of the dynamics of gene frequency changes under selection, by the time resistance becomes noticeable in the field, it is too late to institute resistance management. Thus, while scientific problems remain, some of the major obstacles to dealing with insecticide resistance in Colorado potato beetle relate to implementation of an inconvenient strategy before there is a clear need. However, given the severity of resistance problems in Colorado potato beetle control, these are obstacles which must be surmounted.

Host plant breeding

CURRENT PRACTICES. Host plant breeding for resistance to Colorado potato beetle has not resulted in any commercial resistant varieties (See Tarn, these proceedings). Disease resistant varieties of potatoes are available, as a result of planned breeding (81). While some varieties show different responses to Colorado potato beetle injury (Senanayake, Lactin and Holliday, unpublished), this is a serendipitous, rather than planned, state of affairs.

FUTURE PROSPECTS. Although there is currently no Canadian work in this area, research into Colorado potato beetle resistant potato varieties is an active field (21). Most work has focussed on two mechanisms of resistance. The glycoalkaloid content of solanaceous foliage has long been known to influence Colorado potato beetle preference for, and survival on, host plants. High levels of foliage glycoalkaloids in many of Central and South American Solanum species could be incorporated into the germplasm of the commercial plant to confer Colorado potato beetle resistance. The major obstacle to this approach is the correlation of the concentration of glycoalkaloids in tubers with that in foliage. Because of this, the polygenic inheritance of glycoalkaloid content, and the absence of a method of rapid screening for glycoalkaloid content, interest in this resistance mechanism waned in the mid 1960's.

The presence of abundant glandular trichomes on leaves confers resistance to Colorado potato beetle (17). While many wild Solanum species have such trichomes, most attention has focussed on S. berthaultii Hawkes, which has been successfully hybridized with S. tuberosum (32) (See Pelletier and King, these proceedings). Variety development from such hybrids is underway, and reductions in Colorado potato beetle populations of up to 80% have been achieved, but tuber production is only 50% of commercial varieties (21).

Future host plant resistance work is bound to be influenced by the improving capabilities in gene manipulation; however, the genetic basis of both resistance mechanisms appears to be complex (76,66) and so it may be some time before successful manipulation of these genes is possible. There are over 180 wild tuber-bearing Solanum species known and the USDA has begun to evaluate these for Colorado potato beetle resistance (21); other, as yet unassessed, species in the Andes are threatened by habitat modification, and are in need of protection (42).

Evidence already presented of the rich genetic repertoire of Colorado potato beetle indicates that development of resistant potato varieties will probably not be a permanent solution. Other insect pests have been able to overcome the resistance bred into host plants [e.g. greenbug, Schizaphis graminum (Rondani),(83)] in a relatively short time. Colorado potato beetle confined to S. berthaultii can overcome its resistance in three generations (35). Thus, successful adoption of host plant resistance will require a continuous supply of resistant varieties with different mechanisms of resistance, and these may need to be rotated. A rapid turnover of varieties, such as may be necessary, is very different from the current situation in which a few varieties dominate production and some of them were released more than a century ago. It may be better to utilise a low level of resistance in potatoes and combine this with chemical or other control measures; this is akin to some of the resistance management techniques discussed above, and should prolong the effective life of any resistant variety developed. Combination of resistant varieties with biological control is a promising possibility. It has already been shown that S. berthaultii hybrids are compatible with biological control of aphids (70), however, Edovum puttleri Grissell, an introduced parasitoid of Colorado potato beetle, is not well adapted to S. berthaultii (71). An additional incentive to continue studies of resistance to Colorado potato beetle is that the same mechanisms confer resistance to aphids and leafhoppers (91).

Cultural control

CURRENT PRACTICES. The most common cultural control of Colorado potato beetle is crop rotation. Frequently the alternating crops in the rotation are cereals. In the prairie provinces most potatoes are grown on a 2 - 4 year rotation. In the maritime provinces, continuously cropping of potatoes is more common, but there is a trend in New Brunswick towards increasing the proportion of rotated crops. Where potatoes are continuously cropped, this continues until fertility, disease or insect problems become too severe to continue. In general, crop rotation in the maritimes is not in response to Colorado potato beetle (L.S.Thompson, personal communication) (See Boiteau, these proceedings, for more details).

FUTURE PROSPECTS. In Manitoba, rotation results in the concentration of almost all Colorado potato beetles in the peripheral 50 m of fields (Morris and Holliday, unpublished). This is an excellent situation for spot insecticide treatments, and greatest advantage could be taken of this by using larger fields, or by synchronising rotation in contiguous blocks of small fields.

Rotation reduces the amount of land that can be planted with potatoes at one time, and because potatoes are more profitable than crops with which they might be rotated, this may be a significant obstacle to rotation. Furthermore, because Colorado potato beetle already has the capability to diapause throughout two winters and the intervening summer (31), a preponderance of two year rotational systems might result in selection for this characteristic. Such a response to rotation has recently been identified in the northern corn rootworm, Diabrotica barberi Smith and Lawrence (56).

While it is clear that rotation has some disadvantages, some potato growers do not appear to consider that these outweigh the advantages, even though none take full advantage of the edge effect phenomenon. Rotation is one of the few control techniques other than insecticides which are currently available to all potato growers. Work on optimizing rotation schemes to reduce negative effects, and a comparison of costs and benefits of insecticide alone and integrated insecticide-rotation strategies, could encourage more growers to switch to rotation. This could retard the development of insecticide resistance in Colorado potato beetle, and have positive effects on disease, soil conservation and fertility problems.

Biological control

Although a number of naturally occurring insect parasitoids and predators attack Colorado potato beetle in potato fields, few of them have any significant effect upon populations of the pest (See Sears, Boiteau, these proceedings).

Microbial control shows considerable promise but much work needs to be done before suitable isolates would be available for commercial use, or costs become competitive with synthetic chemicals (See Duchesne and Boiteau, these proceedings).

Other control methods

Plant quarantine has been effective in maintaining some potato growing regions Colorado potato beetle-free. The largest area protected in this way is the United Kingdom; in Canada the same techniques have prevented the pest from becoming established in Newfoundland. In both cases, the protected areas are islands and it is doubtful whether similar techniques could be applied effectively in other circumstances.

Genetic control by the sterile male release technique has been a cost effective method of eradicating the screwworm, Cochliomyia hominovorax (Coquerel) (57,97) from the continental United States. Even so, the investment required was enormous and long term, and brought about by concerted efforts of a number of powerful lobby groups. A sterile male release program for Colorado potato beetle would probably take longer than the 20 years needed for screwworm eradication because of the larger area involved and the longer generation time of the beetle. It is not clear whether the enormous and sustained funding necessary for a joint U.S. - Canadian Colorado potato beetle eradication project would ever be available. However, before that obstacle need be considered, it would be necessary to have a cheap method of mass rearing, sterilizing and releasing Colorado potato beetle.

Economic assessment

The relationship of defoliation to yield loss has received much attention. Early efforts were based upon mechanical defoliation studies (82) and revealed that the yield is most reduced when a defoliation episode occurs at full bloom. Efforts to simulate insect defoliation more precisely confirmed this result and showed that removal of top leaves and non-uniform defoliation of plants within a plot has most effect upon yield (18): defoliation by Colorado potato beetle is characteristically non-uniform among plants and concentrated on the top leaves. Most studies have concentrated on the effects of a short period of defoliation (e.g. 38), rather than season-long insect presence; this approach has demonstrated that the most sensitive stages of the plant are in mid-season, and that late season control may not influence yield, however, it has not allowed the establishment of practical economic injury levels or thresholds. Ferro et al.(26) evaluated the effect of defoliation over a whole season by using insecticide applications to manipulate populations on 'Superior', and observed that although potatoes recover from early season damage if controls are applied in mid season, economic loss occurs because tubers from such plants are smaller. Recently, emphasis has been placed upon the complexity of the Colorado potato beetle - potato relationship and a number of computer simulation studies have been undertaken (e.g. 61,22), however none of these have provided growers with guidance on economic thresholds.

Currently, guidance to growers is limited: in Manitoba, for example, growers are recommended to apply insecticides when leaf damage exceeds 10% (80). This follows from the finding (18) that plants recovered completely from 10% early season defoliation; however, these plants were defoliated once and protected from damage for the rest of the season. Thus 10% must be regarded as an upper bound for the economic injury level. Martel _et al_. (63) used a threshold of 20 larvae per plant for 'Kennebec', but they obtained this from a study in which 20 larvae caused in excess of 10% yield reduction (54).

Economic damage occurs when revenue reduction due to insect injury exceeds the cost of preventing the injury (73). Under current Canadian economic conditions, insecticide costs for a single application are in the range of 1% of the potential revenue for a given field, thus economic damage occurs when injury results in more than 1% reduction in yield. In Manitoba, season-long exposures of 'Norland' to realistic population structures of Colorado potato beetle indicate economic injury levels, assessed at first bloom, of no more than 1 larva per plant (78). The precise values are very susceptible to the combination of insecticide cost and expected yield and price that the grower uses. Preliminary estimates for 'Russet Burbank' (Lactin and Holliday unpublished) indicate higher values for the economic injury level, but still less than 5 larvae per plant. The injury - yield relationships upon which these economic injury levels are based enabled us to make predictions of field losses in unsprayed plots; over four seasons predictions were never more than 10% from the observed field values.

Our findings indicate that only very low levels of Colorado potato beetle do not justify control under Manitoba conditions. In Manitoba, such low levels do occur in the middle of fields, and the economic threshold could be used to delineate the areas for spot insecticide treatments. In areas where the edge effect is not so pronounced, if economic thresholds are similar to those we have derived, their use may not significantly reduce the use of insecticides and thus one potential avenue of resistance management may be closed.

DISCUSSION AND RECOMMENDATIONS

It is probable that two properties of the Colorado potato beetle - potato system will dominate the future of management of the pest. The first is the extreme adaptability of the insect which will probably result in continued instances of resistance to insecticides, and could result in similar phenomena overcoming host plant resistance, rotation, some microbial controls, and possibly other biological controls. The second property of importance is the high revenue associated with potato crops; this justifies expensive control measures, and discourages rotation with other crops.

Two extreme scenarios can be envisaged. One is that the current dependency on chemical controls will continue, with the response to resistance problems occurring after the problems have arisen. In the absence of adequate supplies of new materials, this will lead to higher dose rates, more insecticide applications, escalating costs, and ultimately an unprofitable industry. The other extreme is a rapid switch to integration of control measures including techniques of resistance management. This will require a strong commitment to research and extension, and considerable changes in the way potatoes are grown. While these are extreme scenarios, and the real future lies somewhere between these extremes, it is desirable to steer towards the integrated approach to ensure the best chance for the potato growers of the future.

If integrated pest management is implemented, insecticides will continue to be a part of the management package. Indeed, in the early stages, the main focus of the scheme may be to delay insecticide resistance. However, resistance management by manipulation of insecticides and use of economic thresholds will probably delay, rather than prevent, resistance. Integration of resistance management with rotation, and spot insecticide treatments, where applicable, is a management package for which the technology is already available, and such a package could be implemented quite rapidly.

To perfect this package, information is needed on the compatibility of insecticides of different groups with each other, so that insecticides can be mixed to delay resistance. Equally important is the development of practical economic thresholds and techniques of field assessment so that the spot treatment method can be perfected.

Information is needed on the within-field distribution of Colorado potato beetles in different regions and rotation systems and, where possible, this knowledge should be utilised in improved monitoring and control techniques. One obstacle to adoption of rotation schemes in some areas is the cost of rotation resulting from the need to use less profitable crops for one year in two, or two years in three. Studies of optimal rotation schemes should be undertaken to alleviate this. Economic studies of this integrated pest management package should be undertaken, not only from the point of view of immediate benefits of reduced insecticide use, reduced disease problems, etc, but also incorporating long term benefits resulting from delays in insecticide resistance. Such long term benefits are on a more distant financial horizon than most farmers are able to accommodate, and it may be necessary for governments to intervene to assist farmers wishing to use this management strategy.

The resistance management - economic threshold - rotation package applies only two selection pressures to the Colorado potato beetle population, those of mortality due to insecticides and death during dispersal to new fields. The known adaptability of the insect makes it desirable to increase the number of selection pressures as much as possible. As resistant cultivars, biological control agents, or other controls become available, these should be incorporated into the management scheme both to increase the number of selection pressures and to reduce the required intensity of each selection pressure in the management scheme (e.g. by reducing the number of insecticide applications needed). Increasing the number of selection pressures should reduce the rate at which the insect evolves to overcome each of them, but it would also be wise to continue to develop new insecticides, new resistant cultivars and other new tactics to replace those that the insect evolves to overcome. Thus, there will never be a time when a permanent fixed pest management scheme can be implemented and all further research can cease.

Integrated pest management should not be considered for each pest separately, but for all together. Many of the strategies suggested for Colorado potato beetle management have benefits in the management of other insects, for example resistant cultivars are applicable to aphids and leaf hoppers (91), resistance management techniques will reduce the rate of resistance build-up in all insects subject to insecticide applications, and reduction in insecticide use will allow more natural enemies of aphids and other insects to survive and provide natural biological control. Rotation schemes, if appropriately carried out, provide benefits in disease and nematode management. Although Colorado potato beetle will be a key factor in integrated pest management for potatoes, it is likely that, at times, other management considerations will outweigh those for Colorado potato beetle control. However, sufficient attention must be paid to Colorado potato beetle management to avoid the first scenario outlined above: the destruction of the potato industry because of the cost - or impossibility - of Colorado potato beetle control.

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THE CONTROL OF POTATO FLEA BEETLES, LEAFHOPPERS, WIREWORMS, AND WHITE GRUBS

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ABSTRACT

Control of flea beetles, leafhoppers, wireworms, and white grubs in Canada still relies heavily on the use of insecticides. A few pest monitoring techniques and economic thresholds are either available, or are under development for use in integrated pest management programs in Canada. However, few if any IPM programs are underway, and much needs to be done to prolong the usefulness of pesticides, to reduce the cost of their application, and to reduce environmental contamination.

RESUME

On se sert encore abondamment d'insecticides pour lutter contre l'altise, la cicadelle, la larve de taupin et le ver blanc. Il existe au Canada des techniques de surveillance des ravageurs et des seuils économiques ont été établis, ou sont en voie de l'être, aux fins d'application dans les programmes de lutte antiparasitaire intégrée. Cependant, il y a trés peu de ces programmes en place et il reste beaucoup à faire pour accroître la durée de vie utile des pesticides, pour réduire le coût de leur application et pour freiner la contamination de l'environnement.

INTRODUCTION

Insects are a natural component in any potato field. Some insects are considered serious pests of potatoes, causing reduced yields, interfering with harvest and/or lowering the quality of the crop; some are occasionally serious, and some are not pests at all, some being natural enemies of potato pests. Some of these pests can individually cause crop losses from 50 to 100 percent if allowed to develop unchecked in favourable conditions. The estimated potato crop loss caused by insects in Canada is shown in Table 1 and the annual costs of potato insect control in Canada for all insect pests is indicated in Table 2. In a two year study of the benefits and costs of insect control measures for potato production in Canada, Stemeroff and George (15) demonstrated that for every dollar spent on insect control in Canada from 1960 to 1980, $6.2 were returned to the grower (see McLeod and Tolman, these proceedings).

Table 1. Estimated potato crop loss caused by insect pests in Canada (15).

Pest	Percentage Crop Loss (1960-1980)	
	Without Control	With Control
All potato Insect pests	43.0	6.1

Table 2. Average annual costs of potato insect control in Canada (15).

Insecticide cost	\$9,337,200[a]	(56.2)[b]
Application cost	\$6,706,185	(40.4)
IPM, extension and research costs	\$566,082	(3.4)

[a] 1980 dollars.

[b] % of total cost.

The importance of the group of insects to be discussed here varies from one area to another in Canada. White grub and wireworm damage is usually severe only if potatoes have been planted on land that was previously in sod or pasture for several years; leafhoppers, particularly the potato leafhopper, vary in importance across Canada; and damage from flea beetles varies, depending on the species, etc., and control is not always considered necessary. Although a breakdown of damage caused by these specific pests in Canada was not available, Schwartz and Klasser (14) have put together U.S. information which is shown in Table 3.

Table 3. Estimated losses of potatoes caused by insect pests (14) in the U.S.A., 1977.

Crop Pest	Calculated Yield Loss %[a]	
	Without Control	With Control
Colorado Potato Beetle	46.6	1.0
Flea Beetle	43.3	0.7
Potato Leafhopper	43.2	0.4
Wireworms	4.9	0.2

[a] Total estimated losses (yield loss + cost of control).

It is obvious that some potato pests are causing yield losses in potatoes, and the cost to control these insects with pesticides is increasing. Along with increasing costs of control, several other significant problems are associated with pesticide use in potatoes. These include the development of pesticide resistance and ground water contamination with pesticides. It seems imperative that IPM programs be established that will reduce losses due to potato pests, and reduce some of the problems associated with intensive pesticide use.

The following is a brief discussion of white grubs, wireworms, leafhoppers, and flea beetles as they affect potato crops, and a brief review of some current studies in Canada related to some of these pests.

WHITE GRUBS

Phyllophaga spp. (Coleoptera:Scarabaeidae)

White grubs, the larvae of June beetles and related species, eat large, circular holes in the potato tubers. There are over 200 known host plants. Because damage to potato is generally restricted to developing tubers, infested plants do not normally exhibit the injury, and serious tuber damage may occur before the grower is aware of the problem (Unless skunks dig up the tubers in search of grubs). Damage is most severe in years following peak adult flights and is most pronounced when potato crops follow sod or pasture. Periodic reports of injury are recorded in the Canadian Agricultural Insect Pest review, e.g. in New Brunswick in 1976, Saskatchewan in 1979, etc..

Control of white grubs across the country is generally the same. To avoid injury by white grubs, potatoes should not be planted on land that has been in grass sod for two or more years. If potatoes are to be planted on sod land, especially the year after June beetles are abundant, apply a granular insecticide.

Economic threshold levels do not appear to be worked out although Ontario recommends treating with an insecticide at planting if more than three grubs per square yard are found prior to planting. Summer tillage, especially in the first or second year of the insect's cycle, may give satisfactory control. Special care should be taken when potato crops are planted to fields previously in weedy alfalfa, etc., since these fields tend to have high populations of white grubs. Birds are often effective predators in freshly plowed fields, so sampling is suggested to determine if an insecticide is necessary after plowing.

There are no known studies underway in Canada of the white grub as a potato pest.

WIREWORMS

Eastern field wireworm, Limonius agenus (Say)
Wheat wireworm, Agriotes mancus (Say)
Dusky wireworm, Agriotes obscurus (L.), etc.
(Coleoptera:Elateridae)

Wireworms, the larval stage of click beetles, usually have life cycles ranging from 1 to 4 or more years. They chew shallow to deep pits in tubers, thereby reducing the grade. Young tubers injured by wireworms often become misshapen. Stands can be reduced if seedpieces and young shoots are attacked. Feeding sites are entry points for other insects and disease organisms. In Ontario, damage may be more severe in silt soils than in sandy soils, especially if the soils are not well drained. Wireworms are often accidental pests in that the eggs were laid in some previous crop in the rotation. They are more of a problem in land recently broken from sod; however, some species multiply under continuous land tillage. Wireworms are becoming an increasing problem in the Lower Fraser Valley of British Columbia, especially to table grade growers, and in Manitoba. (Personal Communication, R.S. Vernon).

Because the species vary from area to area, the control practices recommended from one province to another may vary. In considering control, it must be remembered that it takes at least three years for wireworms to develop to an adult stage. The generations overlap so that all age groups and all sizes may be present in the soil at one time. These facts suggest that certain cultural practices and crop rotations should be followed in managing infested soils. If possible, on infested soils, grow crops that are not susceptible to damage from wireworms (e.g. peas and buckwheat). In Nova Scotia, early plowing of grass sod is recommended, followed by several harrowings. Sow grain the next spring, underseeded to clovers. Harvest the hay the next spring, then plow down early, harrow, and repeat the same operation as in the previous year. After harvesting this crop of clover hay, any crop may usually be grown safely.

In Alberta, it is recommended that one avoid planting potatoes for three seasons after breaking sod. Rotate crops with alfalfa and non-grasses and keep the land free of weeds.

A general recommendation seems to be, if one larva per square ($10/m^2$) of soil 6" deep is found, a granular insecticide applied at planting is recommended, if potatoes must be planted. Fonofos and terbufos are recommended in the west. Carbofuran, disulfoton, or phorate are recommended in the Atlantic area, and chlordane, carbofuran, or fonofos were recommended in Ontario in 1986.

There are no known studies underway in Canada of the wireworms as a pest of potatoes.

LEAFHOPPERS

Potato leafhopper, Empoasca fabae (Harr.)
Aster leafhopper, Macrosteles quadrilineatus (FBS) etc.
(Homoptera:Cicadellidae)

The potato leafhopper is widely distributed and frequently very common in the southern parts of Manitoba, Ontario, and Quebec, and it is found also in southern Saskatchewan. In many parts of Ontario, it can be the most significant insect attacking potatoes. Although recorded from most of the provinces, the records, especially for eastern Canada, Alberta, and British Columbia are not reliable. In a 1979-81 survey of arthropods associated with potatoes in New Brunswick (2), the potato leafhopper was not recorded. The species is relatively rare west of Manitoba and there are no reliable records from localities west of Saskatoon (3). The potato leafhopper is known to feed on nearly 200 other species of plants. This insect has long been associated with potato hopperburn (tipburn) (12), but losses caused by it were not fully appreciated until synthetic organic insecticides became available (5). Hopperburn is a physiological condition resulting from potato leafhopper feeding; no pathogens are involved. Both nymphs and adults feed by sucking the sap from the leaves and stems of potato plants, and while feeding, they introduce into the potato a toxin that causes hopperburn. Damage is first evident as a small brown triangular spot at the leaf tip. The margin of the leaf turns brown and rolls inward. Usually, older leaves are first affected, however, severe infestations will affect all leaves. Potato leafhoppers may also be of significance in vectoring a variety of diseases in potatoes.

In a study by Prasad in 1961, it was shown that late nymphal instars cause 2.6 times greater yield losses than the same number of adults (11). Potato leafhopper feeding injury increases plant respiration, depleting reserves available for growth and tuber development. More importantly, there is considerable loss of photosynthetic tissue and occlusion of vascular elements (8). Close linear relationships exist between increasing leafhopper numbers, percent hopperburn, and decreasing yield (13).

The aster leafhopper (six-spotted leafhopper), a leafhopper found throughout all provinces and the Northwest Territories, is a morphologically inseparable species complex of considerable biological, ecological, and physiological variability (4). Although seldom abundant on potatoes, a host on which it cannot reproduce, the aster leafhopper is the vector of purple top wilt disease caused by the mycoplasma-like pathogen, aster yellows. Purple top wilt causes infested leaves to enlarge abnormally and to roll upward. In some cultivars, the foliage takes on a distinctive reddish-purple color. Numerous axillary shoots develop, giving the plant a bunched appearance; wilting and death follow shortly. Tubers from infected plants are soft and either fail to germinate or produce spindly haulms. The adults usually take up the virus while feeding on infected weeds and other plants, and spread it when they feed on healthy potatoes. This is the predominant species of leafhopper on potatoes in P.E.I..

The potato leafhopper and the aster leafhopper are characterized by long distance migration. Both species migrate northward each summer from the overwintering range in the southern United States. No return flight occurs. The potato leafhopper overwinters in the Gulf region from southern Louisiana to northern Florida (9), and each year an influx of adult leafhoppers results from a northward transport on strongly moving warm fronts (10). The aster leafhopper is capable of overwintering in the egg or adult stages in northern regions (e.g. Alberta (1)). Wind-borne migrants are carried northward from overwintering sites in Atkansas and adjoining States and these populations are usually the primary source of the current year's population. About 1% of spring migrants in Alberta are infective for aster yellows (1). Direct damage from sap feeding is probably minimal. The potato leafhopper is not known to survive the winter in Canada.

In Alberta, two other leafhopper species are occasionally problems, the clover leafhopper, Aceratagallia sanguinolenta (Prov.) transmits yellow dwarf to potatoes, while Ophiola dasidus Med., locally abundant in west-central Alberta, transmits witches broom in potato.

The relationship of potato leafhopper density to potato yield was investigated at the University of Guelph in 1986 by Dr. Mark Sears and one of his students. Generally, they found that one leafhopper per sweep resulted in a loss in yield. Leafhopper infestations early in the season appeared to have more effect on yield than late season infestations (Personal Communication).

Potato-infesting leafhoppers do not appear to have any effective natural enemies, so chemical controls must often be applied, although in Manitoba leafhoppers are not considered serious enough to warrant control measures. In areas where insecticides are used to control the Colorado potato beetle and aphids, the potato and aster leafhoppers are usually not a problem. No insecticide treatment is needed during the two weeks prior to plant senescence. Healthy, vigorously growing plants with optimum soil moisture withstand damage better than stressed plants. Systemic insecticides applied at planting often give excellent control through the early season, at least, and may substantially reduce leafhopper-vectored diseases. Potato leafhopper populations build up on certain crops and, after cutting or harvesting, leave the crop to colonize other crops. Therefore, potatoes should not be planted next to alfalfa, grassy headlands, cereal crops, and clover fields.

In Massachusetts, when leafhopper nymphs reach 5 per 50 healthy leaves, treatment is recommended, but economic threshold levels have not been developed for adults (7). No such recommendation could be found for Canadian growers.

FLEA BEETLES

Potato flea beetle, Epitrix cucumeris (Harr.)
Western flea beetle, Epitrix subcrinita (Lec.)
Tuber flea beetle, Epitrix tuberis Gent.
(Coleoptera:Chrysomelidae)

The potato flea beetle is found in every province except British Columbia, the western flea beetle only in Alberta and British Columbia, and the tuber flea beetle only in British Columbia where it is a major concern to growers. Adults of all three species eat small, round, irregular holes in the leaves of potato plants. Larvae of the tuber flea beetle usually feed on the new tubers, but those of the other two species feed mainly on the fine rootlets and only occasionally on the tubers. Larvae feeding on tubers produce narrow, straight tunnels about

0.8 mm in diameter in the flesh of the tubers. Fungi often grow in the tunnels, turning them black or brown. Tunnels of the tuber flea beetle may extend 12 mm into the tuber; when extensive, they make tubers unsuitable for processing. Injury caused by the other species seldom extends more than 6 mm into the tuber-shallow enough that it can be removed by peeling. Larvae of all species may also cause small, raised bumps and shallow, winding trails on the surface of tubers.

Adult flea beetles overwinter in weeds or debris outside the field. In spring, they feed on weeds until potato plants emerge, then fly into potato fields and feed on foliage. Mechanical transmission of some pathogens by flea beetles can occur [e.g. bacterial diseases, spindle tuber, and early blight have been noted (6,7)].

The biggest problem in the Lower Mainland of British Columbia is the tuber flea beetle. As mentioned, unlike the potato flea beetle common to Eastern Canada, the tuber flea beetle can cause severe cosmetic injury to potato tubers at harvest. In the past, growers in this area have relied heavily upon a preventative spray schedule (i.e. endosulfan and methamidophos) to keep populations in check. Although effective at reducing damage, spraying is usually excessive and costly. To develop a more economical control strategy, Dr. Robert Vernon of the Vancouver Research Station is conducting research along two fronts. He has completed considerable work in developing an efficient sampling method for the adult stage of this pest. A reliable approach, employing visual and sweep-net sampling has been developed and demonstrated to growers on a large scale. His program is now being offered to growers by a commercial consulting firm and considerable savings have been realized by subscribing growers. Dr. Vernon's work is continuing in an effort to speed the delivery of this program through computerization, and to further refine the action thresholds currently used (Personal Communication, R.S. Vernon).

In addition, Dr. Vernon is evaluating the use of granular insecticides for control of the tuber flea beetle as an alternative to using foliage sprays. In 1986, several granulars were tested for efficacy and longevity against first generation tuber flea beetles in potatoes grown in three soil types. Only insecticides with systemic properties, such as aldicarb, phorate, and terbufos, gave consistently acceptable control. These systemics were able to kill adults as they fed on potato leaves before oviposition occurred. Non-systemic granulars did not kill feeding adults or significant numbers of soil-dwelling flea beetle larvae.

It was also demonstrated by Dr. Vernon this year that on a commercial scale, granular insecticides used for insect control in table grade potatoes can be reduced by 75%. Granular phorate placed only on the outer rows of a potato field where the major pests such as tuber flea beetles are most prevalent will give excellent early season insect control. This procedure, combined with a back-up pest monitoring service, is a strategy he hopes will reduce the use of granular as well as foliar insecticide usage in the future.

In British Columbia, to provide growers with a multidisciplinary IPM package in potatoes, a computerized approach to making insect as well as potato late blight recommendations has been recently funded. A mobile diagnostic laboratory, outfitted with a microcomputer, will be used to collect and process field collected pest information on a farm-by-farm basis. It is anticipated that insect IPM software will be developed within two years to facilitate rapid handling of insect data collected from potato fields. These programs will process data collected as well as make comprehensive recommendations to the growers. Neither the late blight program, nor the insect monitoring program, as they exist now, would offer enough financial incentive alone to lure a substantial number of growers into contracting a consulting service. Together, however, the insect and disease monitoring programs, made much more efficient through the computer approach, should be a very attractive service for the growers of British Columbia in the near future.

Dr. Neil Holliday of the University of Manitoba has a student working on a project on the economic injury level of the potato flea beetle on an early table potato cultivar (Norland). They find that the phenology of the beetle is such that there is no early season direct damage and that all the direct damage attributable to this insect would result from late season feeding of all adults before diapause. They find direct damage to tubers by the larvae to be negligible. Their results show that, at the densities experienced in Manitoba over the last three years, direct potato flea beetle injury was insufficient to cause measurable loss. Dr. Holliday states that they do have evidence of a relationship between potato flea beetle density and the incidence of potato scab disease; scab is more prevalent when beetles are abundant. They do not, however, have information on the mechanism of the relationship, nor do they know yet the economic significance of the relationship. (Personal Communication, N.J. Holliday)

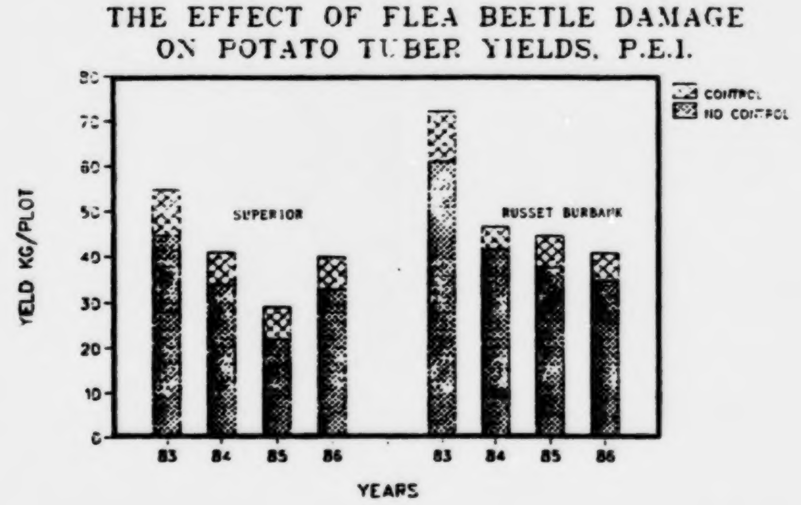
The typical grower practice in Manitoba is to apply late season (end of July) foliar spray application (e.g. carbofuran flowable or endosulfan) to control flea beetles. Certainly, this kills some adults but they do not believe it has any effect upon yield quality or quantity since the defoliation damage which it prevents is not economically significant, and the scab transmission is presumably related to larval activity earlier in the season.

There are two generations of the potato flea beetle in Ontario. The primary damage is caused by the feeding of the overwintered adults in the spring when newly emerged potato seedlings may not have sufficient leaf area to withstand the feeding damage. In severe infestations, the feeding of the second generation adults in August and September may also cause destruction and premature senescence of foliage and reduction in yield. Flea beetles are also suspected as vectors of some virus diseases. (Personal Communication, J. Stewart).

Studies commenced in the early 1980's at the Charlottetown Research Station to (i) determine the impact of potato flea beetle populations on the marketable yield of potatoes, (cvs. Superior and Russet Burbank) and to (ii) develop simple practical criteria for growers to use in determining if and when control of flea beetles was necessary.

From 1983 to 1986, significant yield losses attributed to potato flea beetle feeding were recorded for the cultivar Superior. With Russet Burbank, significant yield losses were recorded in three out of four years (Fig. 1). So by eliminating other pests such as Colorado beetles and aphids through the use of selective sprays and spot spraying, significant yield losses have been demonstrated in Prince Edward Island due to flea beetle feeding. An economic analysis of results of field tests in 1984 indicated that treatments with deltamethrin for flea beetle control generated higher gross margins than the untreated checks (based on experimental plot yields).

Figure 1.

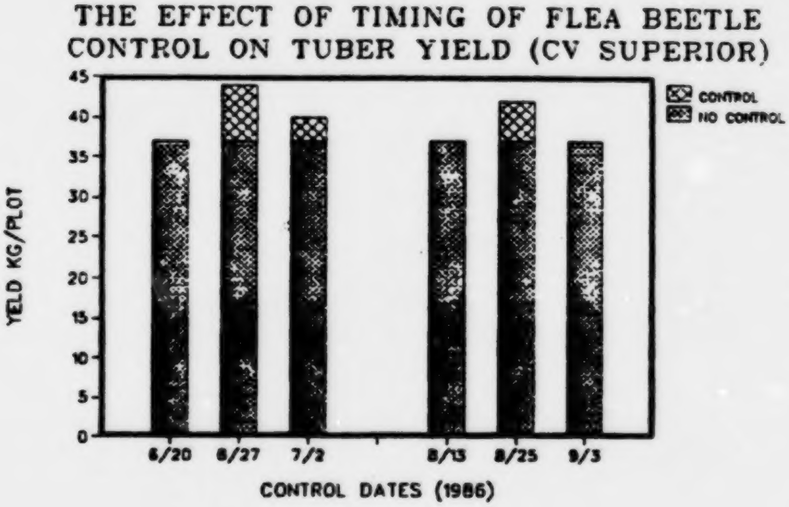


THE EFFECT OF FLEA BEETLE DAMAGE ON POTATO TUBER YIELDS, P.E.I.

Flea beetle damage in the P.E.I. studies was determined by counting all feeding holes in the fourth terminal leaflet of ten plants from the two center rows of each plot. From these damage records, it was hoped that an economic threshold level could be determined. The old Atlantic Provinces recommendation stated that, if an average of 15 holes per 4th terminal leaflet down could be found, a recommended insecticide should be applied. It became apparent that the population densities were extremely variable from year to year (as were the corresponding feeding holes), and low levels of infestation in one year were causing yield reductions, while in another year, very high levels were causing much the same yield reductions. For example, in 1983, 421 feeding holes per 4th terminal leaflet resulted in a yield loss of 16 percent, 531 holes caused a yield reduction of 19 percent in 1984, and, in 1985, 2150 holes resulted in a yield loss of 14 percent. Other factors appeared to be influencing the damage levels. The time of flea beetle damage relative to tuber set or plant maturity appeared to be of significance, etc.. Studies will continue at Charlottetown in an attempt to establish critical populations or damage levels to determine if spraying is necessary.

In another test in 1986, the time of spraying Superior potatoes for flea beetle control was examined. Delaying treatment until 1-2 weeks after adult beetles appeared (first and second feeding periods, respectively) resulted in highest yields in the treated plots as compared with the untreated check plots (Fig. 2).

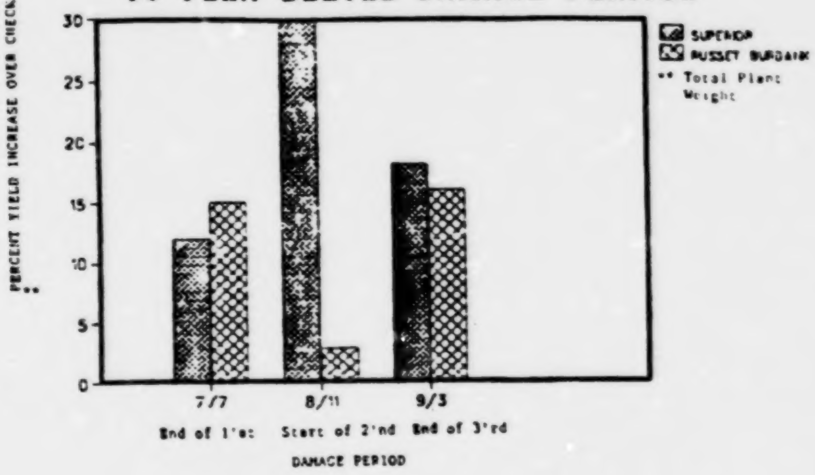
Figure 2.



In another study, total plant growth at various times throughout the growing season was compared from plots where flea beetles were kept continuously under control, and those where flea beetles were allowed to feed all season. Results indicated that, with the Superior cultivar, most of the growth differences occurred around August 11, or the time of the start of the second feeding period. The Russet Burbank plants were apparently able to recover from the effects of the first feeding period (Fig. 3).

Figure 3.

PLANT YIELD INCREASES IN RELATION TO FLEA BEETLE DAMAGE PERIODS



Although not all the data is analyzed from this experiment, the results indicate that it may be possible to reduce yield losses from flea beetles on early varieties like Superior by controlling the insects during the second damage period only. Controlling flea beetles during the second damage period only may prevent yield decreases in later maturing varieties like Russet Burbank.

In a preliminary greenhouse study at Charlottetown in 1986, results suggested that potato flea beetles carry the more aggressive pathogens (Verticillium and Fusarium spp.) with them as they emerge from the soil, and flea beetle feeding enhances the infection of potato plants by these and probably other pathogens. This study will be continued.

On April 1, 1987, Mr. J. Stewart, Biologist-in-Training at the University of Guelph will commence research studies at the Charlottetown Research Station. Mr. Stewart's research will be directed at integrated pest management in potatoes (80%) and cole crops (20%). His initial goals will be to test various action thresholds for potatoes at different locations, as well as to test several compounds for control of the major potato insect pests (anti-feedants). His overall objective will be to determine the relationships between insect pest densities and damage to potatoes in order to establish a workable pest management program for potato growers in the Atlantic Provinces.

DISCUSSION

Potato production areas cover considerable acreage in Canada and demand for the product is high. Although consumer demand is high, so too are consumer expectations; that is, they expect a consistent supply of uniform-sized, blemish-free product. To provide such a product, modern agriculture relies heavily on chemical pesticides to help reduce production costs. However, production costs are rising at a rate faster than returns in many cases. In addition to increased costs of applying pesticides, some control measures are becoming less effective due to pesticide resistance. To prolong the usefulness of pesticides, and to reduce the costs of production, potato producers must soon turn from traditional pesticide application programs to an integrated system of crop protection.

Levels of infestation or infection at which the costs of controlling the pests equals the reduction in yield of the crop if no control is applied must be learned for each key pest affecting potato production. Knowledge of these economic threshold levels is perhaps the most important factor in any successful integrated pest management program. Perhaps the most limiting factor at present to the formulation of sound pest management strategies is a scarcity of these experimentally determined economic thresholds for potatoes in Canada.

Several of the larger potato production areas of the United States have already initiated programs of integrated pest management in potatoes. Some of these techniques need to be tested in Canada. As indicated in this paper, a variety of pest monitoring techniques and economic thresholds are currently available, or under development for use in potatoes in Canada. But much more needs to be done. A study was recently conducted in Ontario to study the feasibility of an integrated pest management program for use on potatoes in that province (Personal Communication, J. Stewart). An attempt has been made recently in Prince Edward Island to obtain funds for a private IPM study in the potato crop. Meanwhile, it appears that pesticides will remain the basis of pest control in potatoes for some time, although some alternative practices are available or under development. IPM will probably not solve all of the problems of potato growers, but it should improve the timing and effectiveness of pesticide applications and should reduce the number of applications required, resulting in higher profits to growers, and fewer problems associated with pesticide resistance and environmental contamination.

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MICROBIAL CONTROL OF INSECT PESTS OF POTATOES

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ABSTRACT

Entomopathogens with most potential for the control of potato pests are reviewed: bacteria (*Bacillus thuringiensis* var. *thuringiensis*, *tenebrionis*, and *san diego*), fungi (*Beauveria bassiana* and *Paecilomyces farinosus*), and a few protozoa and nematodes. The discussion is concerned with their role against aphids and, more particularly the Colorado potato beetle. Microbial control is feasible if developed strategically. The different strains of *B. thuringiensis* are the most interesting entomopathogens and the most promising, considering new research orientations and biotechnological progress. These strains can be used as microbial insecticides for short term control of Colorado potato beetle populations. Fungi, protozoa and nematodes have more limited use and should be considered for long term control.

RESUME

Sans être exhaustif, le présent texte identifie quelques entomopathogènes susceptibles dêtre utilisés pour le contrôle des ennemis de la pomme de terre. L'attention porte sur les bactéries (*Bacillus thuringiensis* variétés *thuringiensis*, *tenebrionis* et *san diego*), les champignons (*Beauveria bassiana* et *Paecilomyces farinosus*) et quelques protozoaires et nématodes. Les pucerons et plus particulièrement le doryphore de la pomme de terre sont les ennemis pour lesquels les entomopathogènes sont discutés. L'utilisation des entomopathogènes est possible selon qu'ils sont utilisés d'une manière stratégique. Les variétés de *Bacillus thuringiensis* sont les plus intéressants entomopathogènes et les plus prometteurs en regard des nouvelles voies de recherche et progrès axées sur les biotechnologies. Elles peuvent être utilisées comme insecticides microbiens pour un contrôle à court terme des populations du doryphore. Les champignons, les protozoaires et les nématodes sont d'emploi plus limité et devraient être utilisés comme agent de contrôle à long terme.

INTRODUCTION

The use of pesticides has played a major role in the worldwide success of the potato crop, *Solanum tuberosum*. Like in other crops, many problems result from a pest control strategy based entirely on chemical pesticides. In many places, the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) and the green peach aphid, *Myzus persicae* (Sulz.) are resistant to a range of insecticides (30, 33, 34, 63). Environmental contamination by aldicarb affects the United States (83) and Canada (77). There are also risks associated with the use of pesticides (pollution, effects on parasites and predators, health of users, etc.). Some insecticides are toxic to *Edovum puttleri* Grissel

(61), an egg parasite of the Colorado potato beetle recently introduced into North America as a potential biological control agent.

It is essential to improve potato management along the lines of integrated pest management so that the environmental impact of controls is eliminated or minimized.

This orientation requires increased knowledge of the biology and economic thresholds of major pests as well as of the development and application of alternate control methods.

In Canada, studies on the use of entomopathogens against potato pests are very few in number. Only a few plot trials have been made with Bacillus thuringiensis Berliner variety thuringiensis (10, 54, 55, 62, 65) and Beauveria bassiana (Bals) Vuill (55). Numerous studies in Europe, USSR, and the United States confirm the potential of entomopathogens against insect pests on potatoes (4, 14, 16, 25, 26, 28, 80).

Microbial control remains an alternative to chemical control alone. The role of entomopathogens has been the object of much discussion (12, 13, 29, 39, 48, 78). Microbial control has evolved considerably (12) and is on the verge of even more important developments due to biotechnological advances (59, 78). Considering the need to intensify microbial control in Canada (59) and to develop new control methods, it is appropriate to review the present situation in order to objectively assess the role of entomopathogens in "Improving Potato Pest Protection", the theme of this Symposium.

ENTOMOPATHOGENS OF INSECTS ON POTATOES

The Colorado potato beetle and the aphids are amongst the worst pests on potatoes (63). Studies on microbial control are concerned primarily with these pests because they are economically important and because of the problems resulting from the use of pesticides to control them.

More than 600 species of natural enemies of Leptinotarsa decemlineata (Say) have been identified (23). Among these entomopathogens, those that have been isolated from natural populations of the potato beetle or from other insects show a variable pathogenicity depending on the organism and its requirements. Almost all groups of entomopathogens are represented: bacteria, fungi, protozoa, viruses and nematodes.

Bacteria of the species B. thuringiensis (B. t.) are very efficient against L. decemlineata. Three serotypes of B.t. are pathogenic: B. thuringiensis var. thuringiensis with the beta-exotoxin (7, 13, 16, 17, 18), B. thuringiensis var. tenebrionis (45, 46) and B. thuringiensis var. san diego (36) with the delta-endotoxin.

Among the fungi, Beauveria bassiana (Bals) Vuill and Paecilomyces farinosus (Dicks.) Brown et Smith are the most important ones (6). Paecilomyces fumosus-roseus (Wize) Brown et Smith and Metarrhizium anisopliae (Metsch) Sorok are also effective against L. decemlineata (6). Other fungi have been isolated from natural populations of potato beetles but they are of secondary importance (6).

Some nematodes are pathogenic against *L. decemlineata* : *Pristionchus uniformis* Fedorko and Stanuszek, Diplogasteridae (27, 70), *Neoplactana carpocapsae* Weiser, Neoplactanidae (58, 79, 81) and some Mermithidae (60). The microsporidia *Nosema gastroidea*, *Nosema equestris* and *Nosema leptinotarsa* (38, 49) are also pathogenic against *L. decemlineata*.

Iridoviruses and one spiroplasma have also been isolated from the Colorado potato beetle. They are not very important; their pathogenicity has yet to be demonstrated against the potato beetle.

Of these entomopathogens, *B. thuringiensis*, *B. bassiana* and *P. farinosus* have been the object of most studies on *Leptinotarsa decemlineata*.

The situation is quite different for the aphids on potatoes. Entomopathogens belong to a complex of fungi. The most important ones in North America are: *Conidiobolus obscurus* (Hall and Dunn) Remaudiere and Keller (= *Entomophthora obscura* Hall and Dunn, = *E. thaxteriana* Petch = *E. ignobilis* Hall and Dunn), *Erynia neoaphidis* Remaudiere and Hennebert (= *E. aphidis* Hoffman), *Entomophthora planchoniana* Cornu and *Zoophthora radicans* (Bref) Batko (= *E. sphaerosperma* Fresenius). Other entomopathogenic fungi have been isolated from aphids on potatoes (75). They are: *Zoophthora occidentalis* (Thaxter) Batko and *Conidiobolus thromboides* Drechsler (= *Entomophthora virulenta* Hall and Dunn). *C. obscurus* is by far the most important entomopathogen, followed by *E. neoaphidis* and *E. planchoniana* (75).

In Canada, very few studies have indicated the presence or efficacy of these entomopathogens compared to the work done in USSR, Europe or the United States. Most recent studies deal with efficacy testing of *B. bassiana* (55) and *B. thuringiensis* (10, 54, 55, 62, 65).

MICROBIAL CONTROL: RATIONALE ON POTATOES

Populations of insect pests can be regulated to economically acceptable levels by a strategic utilization of entomopathogens. Depending on the characteristics of the pest, the crop and the entomopathogen, the microorganisms can be used by introduction, augmentation, inundative release or in an integrated program with other control methods (59).

Some entomopathogens, like *B. thuringiensis*, are essentially used as microbial insecticides for short term control of populations. Others, like viruses and fungi, contribute to a more permanent control by a natural and successive development of epizootics. Whether the effects of the entomopathogens are short term or long term or a combination of both depends on the pathogenicity of the microorganisms, the environmental conditions, the type of crop, and the abundance and behaviour of the pests.

One must not look only for mortality of the host when using microbials. Secondary effects (reduction in longevity and fecundity, change in sex-ratio, change in seasonal development, etc.) caused by the entomopathogens are also very important. Such effects have been reported for the Colorado potato beetle with *B. bassiana* and *P. farinosus* (6).

Many conditions in the system Colorado potato beetle - potato are favorable to the use of entomopathogens:
- The potato crop provides habitat continuity since it is generally grown for a few years in the same field.
- Depending on its phenology and the abundance of the Colorado potato beetle, the potato plant can withstand some defoliation without significant yield loss. The plant has some ability to compensate for defoliation early in the season.
- Only the underground parts of the plant are marketed. Therefore, there is no visible effect of damage by the beetle on the product.
- A large proportion of the population of Colorado potato beetle is continually present in the agroecosystem and the soil is an important element of its biology.

These few considerations facilitate the persistence of entomopathogens in the agroecosystem. They also make more acceptable the slow action of the entomopathogens on the pest resulting from the incubation period and a relatively slow rate of disease build-up. This is an important point because it is this delayed control action that is responsible for hesitation to adopt these new techniques by growers (31). The important role played by the soil in the biological development of the potato beetle provides an interesting environment to exploit with entomopathogenic fungi. Finally, the consumers cannot be affected by the presence of dead or dying larvae on the foliage since aerial parts of the plants are not consumed.

The situation is less favorable to the control of aphids with microbials. Aphids do not persist in the potato agroecosystem. Environmental conditions required for the development of entomopathogenic fungi are not always available within the leaf canopy.

Further, the problem caused by aphids in seed potato production is quite different from the one in processing or tablestock. In the first case, phytosanitary interventions must insure quasi-total protection against aphids that are vectors of viral diseases. In such cases, where chemical insecticides are rarely fast enough, the role of fungi can only be very limited. In tablestock production, aphids rarely affect the crop significantly. The economic threshold for aphids is relatively high.

Depending on the situation, a mycoinsecticide alone or in combination with a chemical insecticide, as well as the natural development of epizootics, can contribute to the economical control of pest populations.

In New Brunswick, between 1981 and 1984, a maximum of 23% of common potato aphids, Macrosiphum euphorbiae (Thomas), in replicated potato plots were killed by naturally occurring fungi. Because the epizootics occurred late in the season -- July 14 and later — it is impossible to conclude whether the decline in aphid numbers observed then was caused by the fungi or by aphid emigration taking place at the same time. Interestingly, levels of infection seemed independent of the density of the host (8) at the normally low aphid population levels (8) but responded to density in resurging populations following insecticide treatment (9). In Ontario, in 1970 and 1971, fungal infections had a negligible effect on the densities of *M. persicae*. A worldwide study of the International Biological Programme observed a maximum reduction of 6 to 7% of *M. persicae* populations with reductions 1% only after the population peak (52).

Over a period of four years, in New Brunswick, only potato aphids were found infected by fungi (8). In neighboring Maine, fungi are also found most commonly in the potato aphid, followed by the green peach aphid and then the buckthorn aphid, *Aphis nasturtii* Kaltenbach. This is either due to a differential susceptibility of the species to the fungi or to the greater motility of the potato aphid, increasing its chances of picking up fungal spores (72). This question has yet to be entirely resolved.

In commercial production, only the potato aphid is likely to require control. The monitoring of the natural prevalence of its fungi and the corresponding cessation of incompatible chemical sprays whenever possible might possibly be a useful means of controlling this aphid. It could also be possible to enhance the natural control of spring migrants by fungi on the overwintering hosts (73). However, it is doubtful that mycoinsecticides could be developed to economically replace chemical insecticides for that purpose.

In spite of some reservations concerning their use, there is no doubt that the complex of *Entomophthora* species is an important one. It cannot be neglected in the development of an integrated pest management program on potatoes (75). In this light, *Verticilium lecanii* and *Zoophthora aphidis* show potential for the control of aphids in Canada (59).

Overall, it is with *L. decemlineata* that chances of success with microbial control are the highest.

ENTOMOPATHOGENS AGAINST THE COLORADO POTATO BEETLE

Microbial control of the Colorado potato beetle seems most promising with bacteria, fungi, protozoa and nematodes.

Bacteria

Bacillus thuringiensis is by far the most interesting microorganism for the control of *L. decemlineata*.

Many laboratory studies have confirmed the susceptibility of *L. decemlineata* to *B. thuringiensis* var. *thuringiensis*, var. *tenebrionis* and var. *san diego* (7, 13, 16, 17, 18, 36, 45, 46). In general, the young larval instars (L1 and L2) of the potato beetle are always more susceptible. For example, with different concentrations of *B. t.* with beta-exotoxin, mortality varies from 75-100% for L1-L2 and 50-100% for L3-L4 with a period of 4-8 and 5-10 days respectively to complete mortality (16). Adults are not very susceptible except that at high concentrations they eventually stop feeding. The exposure of larvae to sub-lethal concentrations can result in teratogenic effects at the adult stage (16, 74).

In the field, repeated applications of beta-exotoxin have reduced the abundance of L3-L4 and adults by 90-100% (17). The effectiveness of the product is always more visible at the younger larval stages. Weekly applications insure an excellent protection in killing L1-L2 larvae before they reach the more destructive larval stages L3-L4 (17).

Similar results have been observed in Quebec, Ontario and New Brunswick in 1984 (54) and in 1985 (10, 55, 62, 65) with the beta-exotoxin (ABG-6162) at concentrations of 35-54 g a.i./ha. From one to five applications of the beta-exotoxin provided satisfactory results compared to the chemical insecticides tested at the same time.

The efficacy of the beta-exotoxin seems to depend on the concentrations used and the number of applications per growing season. At a concentration of 54 g a.i./ha, results obtained with one treatment are only intermediate but two treatments provide good foliar protection (10). To obtain significantly similar yields, 4 treatments were required with the beta-exotoxin versus two with deltamethrin (55). It is also important to indicate that *B. thuringiensis* var. *thuringiensis* is effective against *L. decemlineata.* It is used against the Colorado potato beetle in USSR. However, it is very difficult to establish comparisons among the various studies. Conditions concerning insect abundance, insect development at treatment time, formulations, volumes and pressures at application are often very different. Standardization of trials would be necessary.

Compared to var. *thuringiensis*, laboratory and field tests on var. *tenebrionis* and *san diego* are preliminary. It is impossible to compare the three varieties objectively. The Colorado potato beetle is susceptible to the latter two and the young larval stages are the most susceptible (36, 45, 46).

The first trials took place in 1986 with var. *san diego* in six different regions of the United States and Canada (Quebec). Results are promising for the control of *L. decemlineata* on potatoes. Plant protection was better or equal to that provided by rotenone or fenvalerate + piperonyl butoxide (4). Like for other *B. t.*, the performance of var. *san diego* is caused by its effects on the feeding (inhibition) and mortality of the beetle (4). New field studies with var. *tenebrionis* and *san diego* are necessary. Important research programs will be put in place in Canada and in the United States in 1987, especialy with var. *san diego*.

Presently, neither of these varieties is commercially available in North America. The var. *thuringiensis* is commercially available in Russia where it has been used successfully over the last ten years (16, 18). The var. *tenebrionis* and *san diego* are very recent. In spite of this, the prospect of registration is encouraging, especially for the delta-endotoxin.

All formulations of *B. t.* commercially distributed in North America contain only the delta-endotoxin. They are used in agriculture and in forestry (59).

The mode of action of the beta-exotoxin is considerably different from the delta-endotoxin. The beta-exotoxin inhibits the action of the DNA dependent RNA polymerase. There is a potential risk at the level of the synthesis of the cellular material that could cause mutagenic and carcinogenic effects (64). Even though some mutagenic tests have given negative results (15, 18), the safety of the beta-exotoxin has not been definitely established yet. Further, the beta-exotoxin is not very specific. It is effective against insect species belonging to different orders such as Coleoptera, Lepidoptera, Diptera, Hymenoptera, Isoptera and Orthoptera. It could, therefore, affect beneficial insects (35) such as pollinators, parasites and predators.

On the other hand, *B. t.* var. *tenebrionis* and *san diego* are definitely more specific. They are insecticidal only against some Coleoptera (36, 45) and would have no secondary effects against entomophagous insects (36, 46). Their mode of action is similar to the one for other *B. t.* with delta-endotoxin. Because of the uncertainty about the safety of the beta-exotoxin, var. *tenebrionis* and *san diego* are the most interesting ones at this time.

These two *B. t.* varieties could eventually play an important role in the control of the potato beetle. To be efficacious and economical, these biological products must however be used strategically, that is with consideration of the abundance of the Colorado potato beetle and performances of the products.

This strategic application of *B. thuringiensis* should help increase its efficacy and reduce the number of sprays required. The need to spray more often than with chemical insecticides to obtain similar results makes *B. t.* less competitive and costly.

One could consider using var. *tenebrionis* and *san diego* as follows:

- microbial insecticide applied alone when the abundance of the Colorado potato beetle is low;
- in combination or in rotation with chemical insecticides or fungicides when the abundance of the beetle is moderate to very high;
- in combination with an array of other control methods in an integrated management program. The egg parasite *Edovum puttleri* and the fungus *B. bassiana* are very compatible with *B. thuringiensis*.

This approach, with some adaptations, will also apply to var. *thuringiensis*, if or when registered. A combination of var. *thuringiensis* with var. *tenebrionis* or *san diego* could certainly be economical.

Fungi

There have been many reports of insect populations reduced by fungi. Of these fungi, *Beauveria bassiana* is the most widely used and it affects some 500 species of insects (42). It is frequently used in Russia, where it is recommended mixed with low rates of chemical insecticides. During four consecutive years, Russian workers have observed an average mortality of 92% (30 x 10^9 conidia/g; 1.5 kg/ha) of Colorado potato beetle. Fungi are important natural enemies of the

Colorado potato beetle. *B. bassiana* and *P. farinosus* are the two most important species isolated from natural populations of potato beetles in Poland (6). Many studies have been undertaken in Poland on the short and long term incidence of these two species in the Colorado potato beetle and on the identification of factors affecting their efficacy (6).

The interest for fungi in biological control is based on their possible utilization as mycoinsecticides and on the development of natural epizootics from enzootic populations or introduced and augmented populations. Compared to *B. thuringiensis*, this offers a new dimension to integrated pest management programs. This is especially advantageous for large populations of Colorado potato beetles and when there is more than one generation per year. Epizootics perturb populations considerably, both on the short and long term, by creating numerous secondary effects.

Many laboratory and field studies have in fact demonstrated the susceptibility of the Colorado potato beetle to *B. bassiana* (40, 69) and its efficacy as a mycoinsecticide (14, 25, 26, 80). In a comparative test with *B. thuringiensis* var. *thuringiensis* and a few chemical insecticides, *B. bassiana* (10^{10} conidia/g; 3.7 kg/ha), with a threshold of 10 larvae/plant, gave intermediate results and required only two treatments compared to four for *B. t.* var. *thuringiensis* (55). The yield was lower than with *B. t. thuringiensis* but not significantly so. These results stem from the only known Canadian study with *B. bassiana* against the Colorado potato beetle. Like with *B. thuringiensis*, Canadian efforts with *B. bassiana* and in microbial control are, unfortunately, too uncommon even though this fungus is considered an alternative and a complement to chemical insecticides (67).

To optimize the number of applications of *B. bassiana*, a strategic approach is required. Some approaches taking into consideration the abundance of the potato beetle and the slow killing action of the pathogen have already been suggested (14, 25, 40). A mixture of *B. bassiana* with different rates of chemical insecticides is a reasonable approach for moderate to very high populations (14, 25, 40). This way, a portion of the population is immediately destroyed by the insecticide without synergistic effects but with a greater susceptibility of the larvae to the disease (25).

If *B. bassiana* is used at rates of 7.5×10^{11}, 1.6×10^{13} and 2.0×10^{14} conidia/ha. the potential mortality will be 50, 90 and 99% respectively. However, a rate of 2.5×10^{10} should be sufficient (mortality rate of 10%) early in the season. In this case, control will be achieved by epizootics following the application of *B. bassiana* (40).

In spite of these results, *B. bassiana*, like other fungi, is unfortunately unstable under certain environmental conditions (42). Many abiotic (temperature, humidity) and biotic (strain, rate, larval stage, molt) factors affect the mortality rate of the potato beetle and can delay the time of infection (24). The molting and the temperature are the two most important factors (24). The humidity is also quite important (14, 24). Field successes with the mycoinsecticide *B. bassiana* were essentially attributable to higher humidity after treatment (14). Irrigation may have to be recommended when considering *B. bassiana* for the control of the Colorado potato beetle (14).

Even though there is intensive production of *B. bassiana* in the United States and elsewhere, the coming on the scene of *B. thuringiensis* var. *thuringiensis*, var. *tenebrionis* and var. *san diego* could change the perspective considerably. *Bacillus thuringiensis* is definitely more stable than *B. bassiana* and more likely to be used in an integrated control program. Also, *B. bassiana* is much less compatible with insecticides and fungicides than *B. thuringiensis*. In fact, *B. bassiana* is somewhat incompatible with the fungicide mancozeb (19, 50) and the insecticides permethrin, fenvalerate and endosulfan (2), all commonly used in potato production.

However, *B. bassiana* remains an interesting mortality factor against the Colorado potato beetle. It is included in the list of systems of particular interest for the control of insects of agricultural importance in Canada (59).

A new ecological concept considers and encourages the development of the disease in sites most favorable to infection and treatments. Soil application is the most promising approach (6, 66). The soil is more favorable because it offers a more sustained level of relative moisture suitable to the development of the fungus. The soil is also an environment essential to the development of the Colorado potato beetle. A few studies exploiting this theory have been realized recently with some success (6, 66, 80, 82).

The application of *B. bassiana* to the soil affects not only the pupae but also the adults (80). Soil applications against the first generation of pupae reduced the population by 74%. Adult emergence was reduced by 66.2%. Adults emerging are affected by *B. bassiana* at a rate of 26.3% comparatively at 3.9% in controls. The second generation is also reduced some 77.3%.

There are also cumulative effects on the populations of Colorado potato beetles. Mortality by *B. bassiana* has been detected as much as two years after treatment (6, 67, 82). Implications are:

- controls overwintering numbers;
- affects resistance of overwinterers to winter;
- reduction of feeding by adults which are smaller;
- reduction in the longevity of adults and number of eggs.

Similar effects have been observed in Poland with *B. bassiana* and *P. farinosus* present in the soil (6, 44, 82). Introduction of these two species of fungi with the nematode *Pristionchus uniformis* delays the emergence of adults in the spring and reduces the viability of eggs.

The direct and indirect effects of the fungi *B. bassiana* and *P. farinosus* cause not only a reduction but also a long term control of populations of Colorado potato beetle. Fungi can therefore be used in combination with other control methods against the Colorado potato beetle.

In fact, P. farinosus could be combined with B. bassiana. The first is more tolerant to low temperatures and is the dominant species against L. decemlineata early in the spring (6). B. bassiana dominates later in the vegetative phase when temperatures are warmer. Infection with B. bassiana is best at 20°C even though the optimal temperature for the beetle and the fungus is at 25°C (24).

The pathogenicity of many strains of P. farinosus is well known (43). P. farinosus reacts to herbicides such as linuron by an increased pathogenicity. Linuron reduced the pathogenicity of B. bassiana (6). The two fungi persist better in the soil when they are introduced together rather than separately (5). The relation between their enzymatic activity and virulence (68) should prove a useful tool for the screening of the most virulent strains.

Protozoa and Nematodes

This group has received the least attention, especially with the Colorado potato beetle. Studies are fewer in number and results are often inconclusive regarding their potential in microbial control.

Like the fungi, they can affect pest populations in the short or long term. A few references report on the incidence of these pathogens in the potato beetle (6, 27, 38, 49, 58, 60, 70, 79, 81).

In spite of some positive effects, one must know the range of applicability of these pathogens to exploit them rationally and economically.

Their utilization as microbial insecticides remains very limited. Protozoa are produced only in vivo, making large scale production more difficult (42). They are more appropriate for long term control (59). Nematodes are sensitive to solar rays and dessication (6). Dessication is an especially important limiting factor. Foliar applications of nematodes have had very little effect against the Colorado potato beetle (81). Anti-dessicants are available. Infection rates of Colorado potato beetle by Neoplactana carpocapsae were increased by 30 - 60% with various anti-dessicants (42). Also, a better protection is obtained by evening applications (32, 53).

Protozoa and nematodes do offer some potential. A choice will have to be made among the different pathogens of the Colorado potato beetle. The introduction and the augmentation of the most virulent pathogens in combination with other methods of control could have a significant impact on populations of potato beetles.

Spores of protozoa are persistent and can be transmitted by the adults to their progeny transovarially (42). There are many examples of secondary effects following the introduction of the nematode P. uniformis into the soil (6). This nematode is an interesting addition to the fungi B. bassiana and P. farinosus (6). It is also extremely resistant to agrochemicals (6).

In summary, it is quite evident that the bacteria and the fungi can contribute effectively to the control of the Colorado potato beetle. The action of the other pathogens cannot be overlooked but their utilization remains very limited.

RESISTANCE TO MICROBIALS

In spite of their potential, microbial agents of control are not immune to the problems facing chemical insecticides. A lepidopteran grain pest, for example, has developed resistance to *B. thuringiensis* var. *kurstaki* (56). In a 1971 review, Burges (13) concluded that, in the laboratory, slight resistance to beta-exotoxin had been shown in Diptera (*Musca domestica*) (47). Thus, substantial resistance to the spore-crystal complex of *B. t.* in lepidoptera is not to be expected in the field within a reasonable time (47). A nematode of the Colorado potato beetle was observed to cause an increase in the number of hemocytes, a defensive reaction of the beetle (71). As we learn more about the potential of microbiological products for the control of potato pests, we are likely to discover more counter-reactions from the pests. This should encourage us to consider them as an adjunct to existing control techniques within rational management programs rather than replacements.

REGISTRATION OF ENTOMOPATHOGENS

Like chemical insecticides, entomopathogens must be registered by Agriculture Canada. None of the entomopathogens of the Colorado potato beetle and the aphids are presently registered in Canada. The few entomopathogens registered in Canada (59) (twenty-three formulations of *B. t.* var. *kurstaki*, three formulations of *B. t.* var. *israelensis* and two viruses) should, however, facilitate the registration of other pathogens.

Also, the recent consultation by Agriculture Canada about guidelines for the evaluation of the safety and acceptability of natural microbial pesticides (bacteria, viruses, fungi and protozoa) for their registration shows how important entomopathogens are becoming for pest control programs (3). The guide is inspired from the directives of the Environmental Protection Agency (EPA), the United Kingdom and World Health Organization. The guide includes supplementary requirements specific to the Canadian environment, including field tests and efficacy testing, depending on the mode of utilization.

Microbial agents must satisfy the following requirements:
- selective to the target pest;
- absolutely not toxic to man;
- absolutely not toxic to domestic animals, fish, wild animals, non target insects or useful plants;
- no effect on water quality;
- do not accumulate in non target organisms;
- easily produced;
- easily disseminated;
- persistent after introduction;
- effective in the environmental conditions characteristic of the site where they are to be used;
- detection methods simple to use (quantitative and qualitative and enabling detection of the pathogen at low density).

It will, therefore, be necessary to take into account these criteria when selecting entomopathogens and their mode of utilization. The literature on microbial control can already help us to make rational choices.

SAFETY AND COMPATIBILITY

Safety and compatibility are criteria as essential as efficacy when selecting microbials. The criteria proposed by Agriculture Canada for the registration of entomopathogens should answer the question of safety. Further, none of the tests done to date suggest a risk associated with the entomopathogens and nematodes being developed for microbial control (59).

However, no guideline for the registration of nematodes is available in Canada or in the United States (59). No formulation of B.t. with exotoxin is registered in Canada (59). This is why it is important to accumulate data on the different groups of entomopathogens. In many cases, the use of entomopathogens in combination with other methods of control remains the best approach. Consequently, it is important to take into account the compatibility of the different entomopathogens with the other methods of control.

Viruses and *B. thuringiensis* are generally less affected by chemical pesticides than fungi and microsporidia, and insecticides have less effects than fungicides (59). Some examples of incompatibility between *B. bassiana* and chemical pesticides for the Colorado potato beetle have already been mentioned.

It is the same story with the fungi of potato aphids (75). Selective use of chemical pesticides is necessary (59). Strains of entomopathogens resistant to chemical pesticides could be developed (75).

Entomopathogens, parasites and predators are usually very compatible, especially if the stage of the target pest is different. The egg parasite, *E. puttleri*, could constitute an excellent combination with most entomopathogens of the Colorado potato beetle because none attack the egg stage.

In all cases, the success of the combined action of the control methods depends on the judicious choice of methods and their harmonious integration more than on the number of methods put in place.

OUTLOOK AND ORIENTATIONS

New avenues of research and progress are apparent: biotechnologies applied to agriculture. Biotechnology will change the world market of phytosanitary products (57). Entomopathogens will benefit from these new biotechnologies, especially from genetic engineering. It should result in an even more advantageous potential in the very short term.

Because of their simplicity and susceptibility to genetic manipulations, bacteria, e.g. B. thuringiensis, are among the most promising microbial agents (21, 51, 78). Even though this research is still very recent, the scientific literature already offers interesting possibilities (1, 11, 21, 22, 37, 51, 59, 76, 78).

The interest in the utilization of B. t. var. tenebrionis and var. san diego against the Colorado potato beetle is, therefore, well justified. New products of different toxicity and specificity and the insertion of genes from B. t. into plants have already been considered with B. t. var. san diego (36).

If the integration of microbial control into potato pest control is to progress rapidly and effectively, orientations must be established for research, education, information and also in politics:

*Research:

- complete our knowledge of potato pests and economic thresholds and develop a program of integrated control;
- develop alternative control methods that are effective, economical and safe;
- identify entomopathogens present in natural populations of pests and verify their pathogenicity and virulence;
- standardize laboratory and field tests for entomopathogens;
- verify under our conditions the applicability of controls with B. thuringiensis, B. bassiana and P. farinosus;
- identify new entomopathogens more virulent and capable of providing longer term control;

*Education and information:

- promote the need to develop control methods as alternatives to chemical pesticides;
- promote entomopathogens and their acceptability;
- facilitate access to information on microbial control and entomopathogens by the creation of computerized data banks.

*Politics:

- increase person years in research and the funding of alternate control methods;
- insure governmental expertise along the lines of biotechnological developments;
- facilitate on a national scale collaboration among scientists so that efforts and resources can be better integrated;
- facilitate exchanges of scientists with countries already very involved in microbial control, such as Russia, Poland and France.

CONCLUSION

The improvement of pest control on potatoes must be based on a set of control methods that are efficient and very safe for the environment. Numerous mortality factors slow down or prevent the phenomenon of pesticide resistance and ensure better stability of interventions. In this sense, entomopathogens are mortality factors with an important role to play in the regulation of populations. Their natural presence in populations and their strategic utilization cannot be ignored in an integrated pest management program.

The use of entomopathogens against potato pests is definitely possible. *B. thuringiensis* is certainly the entomopathogen offering the most potential. It is now necessary that efforts in microbial control on potatoes, such as those taking place in Russia, Poland and France, be rapidly implemented in Canada.

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CONTROL OF NEMATODES

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ABSTRACT

The root lesion nematode is the most important nematode pest of potatoes in Canada. Control of this nematode is heavily dependent on chemicals since crop rotations are usually not effective, and suitable resistant cultivars have not been developed. Reliable economic thresholds which can be incorporated into pest management programs have been developed for the root lesion nematode. The two potato cyst or golden nematode species have not been detected in the mainland areas of Canada and are not a factor in potato production. Strict quarantine measures restrict the movement of these pests from Newfoundland and Vancouver Island to the mainland. Resistant potato cultivars, effective crop rotations, nematicides, and information on economic thresholds are available if potato cyst nematodes are ever detected in the major potato areas of Canada. The northern root-knot nematode occasionally causes minor yield reductions in potatoes, and the potato rot nematode is not a problem at the present time.

RESUME

La nématode radicicole est le plus important nématode de la pomme de terre au Canada. On compte beaucoup sur les produits chimiques pour lui faire la lutte car les rotations culturales sont habituellement inefficaces et aucun cultivar résistant convenable n'a encore été mis au point. On a toutefois réussi à établir des seuils de rentabilité fiables pouvant servir dans les programmes de lutte antiparasitaire. Les deux espéces de nématode à kystes ou nématode doré n'ont pas été décelées dans les régions de l'intérieur du Canada et ne sont pas un facteur dans la production de la pomme de terre. On parvient à restreindre la propagation de ces ravageurs grâce à des mesures de quarantaine rigoureuses pour les tubercules provenant de Terre-Neuve et de l'Ile de Vancouver. Si jamais des nématodes a kystes étaient décelés dans les principales régions productrices de pomme de terre du Canada, nous serions en mesure d'offrir des cultivars résistants, des méthodes de rotation des cultures efficaces, des nématicides et de l'information sur les seuils de rentabilité. Le nématode des racines du nord influe parfois légèrement sur les rendements des superficies de pomme de terre et le nématode de la pourriture nématique ne pose pas de problème à l'heure actuelle.

INTRODUCTION

There are approximately 70 nematode species that are associated with potatoes throughout the world (12). Most of these are of little or no economic importance in potato production, but a few species do have a major impact and in some cases the destruction approaches 100%. Since nematodes usually attack underground structures such as roots and tubers, there are no concise diagnostic symptoms on above-ground portions of plants to signify that nematodes may be the major cause of poor growth and reduced tuber yields. The amount of damage to potatoes by nematodes depends on several factors such as nematode species involved, size of the population, susceptibility of the host, soil type and moisture conditions. Injury by nematodes may be detected by the presence of cysts, galls, lesions, and deformed roots. After a few weeks, however, roots are decayed by secondary invaders such as bacteria and fungi, and the original injury is not obvious. Consequently, nematode damage to potatoes has often been attributed to other factors. For example, attack by large populations of nematodes usually causes unthrifty top growth and yellowing of foliage. These symptoms can also be caused by lack of nutrients or moisture, and the importance of nematode invasion in potato production has often been overlooked (5).

There have been no detailed estimates in Canada of yield losses in potatoes due to nematodes. However, Table 1 shows the estimated loss figures in potatoes due to nematodes in the United States. This information was drawn from literature reviews, annual reports of state and federal laboratories, data from storage banks of the United States Department of Agriculture, and from direct contact with state and federal nematologists, plant pathologists, and crop production specialists, as well as chemical industry representatives (7). Based on this information, it is estimated that 10% of the potato crop in the United States is lost annually because of nematodes. The figures in Table 1 are preliminary, but it is reasonable to assume that the estimated losses for potatoes are also applicable to the Canadian situation.

Table 1. Estimated annual losses[1] in vegetable crops and potatoes due to nematodes in the United States (7).

Crop	Estimated % loss due to nematodes	Average estimated losses in production[2]
Vegetable (24 crops)	11	3,475,000
Potatoes	10	1,280,000

[1] Based on 1962-1968 data.

[2] Metric tonnes.

The following is a brief description of the nematode groups or species that are important pests in potato production. Research studies which have been conducted, or are currently underway in Canada, are outlined.

ROOT LESION NEMATODES

Since their first description as parasites of potatoes (34), root lesion nematodes (Pratylenchus spp.) have been reported with poor potato growth in many countries (5). At least seven species of root lesion nematodes are known to attack potatoes (11). Maximum damage occurs on sandy soils, since these nematodes prefer this type of soil, and also because sandy soils are suited for potato culture.

Root lesion nematodes are migratory endoparasites of roots. Adult females lay eggs in roots or soil. Second-stage juveniles hatch from eggs, invade roots, and develop through the third and fourth stages to adults. Second, third, and fourth stage juveniles, as well as adult males and females are all capable of invading and migrating through roots. A life cycle takes 20 to 60 days to complete, and depends primarily on the condition of the host and on temperature (36).

Above-ground symptoms caused by high populations of root lesion nematodes resemble typical plant stress, and the causes are often wrongly attributed to lack of water and nutrients. Root lesion nematodes attack roots primarily but there are a few reports of damage to tubers when populations are very high (9,19,34).

It is generally accepted that the most important nematode parasite of potatoes in the northeastern United States and in Canada is the root lesion nematode, Pratylenchus penetrans (Cobb, 1917) Filipjev & Sch.Stek., 1941. Surveys of potato fields on Prince Edward Island (14) and in Ontario (26) indicated that this species was prevalent.

In the early seventies, Olthof and Potter (25) in Ontario conducted studies on the relationship between numbers of P. penetrans and crop losses in potatoes. These investigations were considered essential for diagnostic and advisory services, and in efforts to increase crop production efficiency without using chemical control measures unnecessarily. It was shown in microplots (20 cm internal diameter and 30 cm deep) that densities of 6,000 and 18,000 nematodes per kg of soil at planting reduced marketable tuber yields by 35% and 42%, respectively, relative to the uninfested control. Olthof and Potter (25) concluded that root lesion nematode populations in excess of 2,000 per kg of soil at planting were capable of causing economic losses in tuber yields. A study on Prince Edward Island, which examined the relationship between numbers of P. penetrans at planting and the resulting percentage tuber yield increases of potatoes when aldicarb (2-methyl-2-(methylthio)propionaldehyde O-(methylcarbamoyloxime) was applied, agreed quite closely with the Ontario findings (18). Table 2 shows that populations of about 2500 nematodes per kg of soil at planting were having a noticeable impact on yields.

Table 2. Numbers of *Pratylenchus penetrans* at planting and corresponding yield increases of potato cv. Superior after treatment with aldicarb (18).

Year	Numbers of Nematodes per kg of dry soil at planting	Yield increase[1] (%)
1980	500	3
1981	1900	3
1982	2500	13
1979	3100	8
1983	3900	25
1978	6000	47
1984	17000	28

[1] Difference between untreated plots and plots treated at planting with aldicarb at 2.24 kg active ingredient per hectare.

Table 3. Influence of 1,3-dichloropropene and aldicarb on numbers of *Pratylenchus penetrans* in potatoes[1] (15).

Treatment	Rate/ha	Number of nematodes at harvest[2] per kg of soil	Number of nematodes at harvest[2] per g of root
1978			
Check	0	5160a[3]	3250a
1,3-dichloropropene	102 L	3880a	2080a
	284 L	3690a	1660a
Aldicarb 10G	2.24 kg[4]	530b	80b
1979			
Check	0	6960a	4570a
1,3-dichloropropene	102 L	810b	3450a
Aldicarb 15G	3.36 kg	10c	240b
1980			
Check	0	3110a	910a
Aldicarb 15G	1.68 kg	370b	30b
	3.36 kg	30c	10b

[1] Combined data from several cultivars.

[2] Number of nematodes at planting in 1978,1979, and 1980 were 6010,3090, and 510 per kg of soil, respectively.

[3] Values in each column followed by the same letter are not significantly different at P=0.05 (Duncan's MRT).

[4] Active ingredient for the aldicarb rates.

The study of damage thresholds was accompanied by studies on the control of nematodes by nematicides. A three year experimental plot study on Prince Edward Island indicated that aldicarb applied in the row at planting reduced the size of root lesion nematode populations substantially (15). However, 1,3-dichloropropene applied approximately three weeks before planting did not always reduce nematode populations significantly (Table 3). In the same study, 1,3-dichloropropene and aldicarb were associated with tuber yield increases of about 40% (derived from Table 4) in Superior and Sebago, and 1,3-dichloropropene at 102 litres per hectare also increased Kennebec yields in 1978. There were no significant yield responses to the nematicide treatments in 1979 and 1980 when the root lesion nematode populations at planting were smaller.

Table 4. Influence of 1,3-dichloropropene and aldicarb on potato yields (15).

		Total yield - tonnes/ha[1]				
Treatment	Rate/ha	Kennebec	Superior	Sebago	Russet Burbank	$\bar{S}x$
1978						
Check	0	36.9	21.9	19.4		
1,3-dichloropene	102 L	42.9	30.6	30.7		
	284 L	37.6	29.0	29.0		
Aldicarb 10G	2.24 kg[2]	39.9	32.1	28.2		±2.02
1979						
Check	0	32.2	27.8		20.8	
1,3-dichloroprene	102 L	33.5	25.3		21.7	
Aldicarb 15G	3.36 kg	31.4	29.9		23.6	±2.69
1980						
Check	0	40.1	39.6	38.7	36.3	
Aldicarb 15G	1.68 kg	40.1	42.4	39.2	37.4	
	3.36 kg	39.9	39.2	35.9	35.4	±2.10

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[1] Each yield value is the mean from 4 replicates (plots). Each plot was 6 metres long with 4 rows.

[2] Active ingredient for aldicarb rates.

Aldicarb is widely used at the present time for nematode control in potatoes. However, problems with groundwater contamination have occurred in certain locations, such as Long Island, New York, where extra heavy applications of aldicarb (3 to 5 kg active ingredient per hectare) were used to control insects and nematodes (22). On the other hand, oxamyl (N,N-dimethyl-2-methylcarbamoyloxyimino-2-(methylthio) acetamide), a compound with properties similar to aldicarb, has not received adverse publicity to date. Therefore, Olthof et al. (28) conducted microplot experiments on the effect of oxamyl on root lesion nematode populations and tuber yields. Their results showed that nematode populations were reduced dramatically shortly after treatment, and though nematode populations increased later in the season, tuber weights were 31% to 73% greater in the treated plots (Table 5).

Table 5. Soil and root populations of Pratylenchus penetrans in microplots[1] grown to potatoes cv. Russet Burbank at Jordan Station, Ontario (28).

	Number of nematodes[2]				
	per kg of soil				
Oxamyl treatment (24% act. ingred.)	At planting	Eight days after planting	At harvest	Per g of root at harvest	Wt. (g) of tubers/ microplot
0	10700a	10500a	48200a	5000a	837a
9 L/ha[3]	10400a	200b	43500a	5400a	1275bc
18 L/ha[3]	10900a	70c	25700a	2800a	1094b
9 L/ha + 9 L/ha[4]	10800a	260b	19900a	1500b	1449c

[1] Twenty cm in diameter and 30 cm deep.

[2] Each value is the mean of 20 replicates. Column means followed by the same letter are not significantly different at P=0.05 (Duncan's MRT).

[3] Preplant treatment.

[4] Preplant treatment plus five foliar sprays.

A three year study on Prince Edward Island also examined the effect of oxamyl, as well as aldicarb, on nematode populations and tuber yields (17). Although aldicarb depressed nematode populations more than oxamyl, the overall effect of aldicarb on tuber yields was not significantly different from that of oxamyl (Table 6). In general, the nematicide treatments increased yields of Superior by 12-38% in comparison to the untreated checks. These results together with the work in Ontario (28) indicated that oxamyl is a useful alternative to aldicarb for root lesion nematode control in potatoes in Canada.

The relative host status and susceptibility to damage of different potato cultivars to root lesion nematode has recently been investigated in Ontario (27,29). Microplot experiments determined that a relatively low initial density of 1850 nematodes per kg of soil reduced the yield of marketable tubers of Russet Burbank by 16% (27). Marketable tuber yields of five other cultivars, Kennebec, Monana, Norchip, Superior, and Yukon Gold did not differ significantly between the nematode-free plots or nematode-infested plots. When the experiment was repeated using relatively high population levels of 9800-11500 nematodes per kg of soil, the yields of all cultivars were reduced and Superior was the most susceptible (Table 7).

Table 6. Effects of soil treatments with oxamyl and aldicarb on numbers of Pratylenchus penetrans in soil and roots of potatoes[1] and on tuber yields of cv. Superior (17).

Treatment[2]	1982	1983	1984
		No. of nematodes per kg soil	
Check	1390a[3]	1660a	10670a
Oxamyl	170b	310b	1350b
Aldicarb	60c	90c	540c
		No. of nematodes per g root	
Check	6980a	8560a	11000a
Oxamyl	2560b	2160b	11800a
Aldicarb	1650c	730c	7230a
		Marketable tuber yields (tonnes/ha)	
Check	40.3a	23.5a	31.2a
Oxamyl	45.1b	28.2b	42.9b
Aldicarb	45.0b	29.3b	39.9b

[1] Nematode data obtained from several cultivars.

[2] Oxamyl and aldicarb applied in granular form at 2.24 kg active ingredient per hectare.

[3] Means of 4 replicates within each column followed by the same letter are not significantly different by Duncan's MRT (P=0.05).

Table 7. Percentage loss in tuber yields of six potato cultivars due to Pratylenchus penetrans (29).

Cultivar and maturity	Percentage loss[1]	
	Total yield	Marketable yield
Medium (118 days)		
Superior	73	73
Yukon Gold	32	25
Monana	46	46
Late (139 days)		
Norchip	45	43
Kennebec	50	55
Russet Burbank	57	61
SEM	4	6

[1] Average difference between nematode-infested soil (9800-11500 nematodes /kg soil at planting) and nematode-free soil. Based on 20 replicates.

Observations from field plots on Prince Edward Island agreed in general with the Ontario studies and confirmed that Superior is more susceptible than Russet Burbank, Kennebec, or Shepody to damage from root lesion nematodes (15,17). There are no potato cultivars which are resistant to root lesion nematodes, but this information should be useful in the selection of suitable cultivars when root lesion nematodes are a problem and use of nematicides is not feasible.

Root lesion nematodes have a wide host range and crop rotations are usually not successful (5). However, field studies on Prince Edward Island indicated that red clover (*Trifolium pratense* L.) and timothy (*Phleum pratense* L.) generally were better hosts than annual ryegrass (*Lolium multiflorum* L.) (16). The information in this study should be useful for crop and pest management programs since the substitution of ryegrass for red clover or a red clover-timothy mixture might alleviate some of the root lesion nematode problems in the Maritime provinces. Annual ryegrass cultivars grow well in the Atlantic region and agronomic studies have suggested that they can be grown successfully for pasture and conserved forage (20). Therefore, growers wishing to rotate a forage crop with potatoes have the option of using ryegrass instead of red clover or a red clover and timothy mixture.

POTATO CYST NEMATODES

The most destructive nematodes world-wide are the potato cyst nematodes, *Globodera rostochiensis* (Wollenwebber, 1923) Behrens, 1975, and *G. pallida* (Stone, 1973) Behrens, 1975. Potato cyst nematodes are sedentary endoparasites with distinct sexual dimorphism. At maturity, females die and their body walls become tough protective cysts containing up to 500 eggs. Once formed, cysts lie dormant in soil until conditions are suitable for second-stage juveniles to hatch from eggs and enter the host roots. Feeding by the nematodes induces cell enlargement and breakdown of cell walls which causes formation of large syncytial cells with dense cytoplasm (13). The second-stage juveniles become sedentary and molt to third-stage juveniles. Two more molts lead to the development of vermiform males or saccate females.

Potato cyst nematodes were first reported in North America in 1941 on Long Island, New York (6). They were subsequently found in Newfoundland in 1962 (23), and on Vancouver Island in British Columbia in 1965 (30). In 1967 *G. rostochiensis* was detected in western New York State. There also have been a few isolated occurrences in Delaware and New Jersey (21). Brodie (5) postulates that the pattern of potato cyst nematode infestation and spread in Europe which took place about one century ago is now being duplicated in North America.

Potato cyst nematodes do not cause economic losses in Canada and the United States because of their limited distribution and population size. However, potato cyst nematodes sometimes cause severe losses in other regions of the world. Even where infestations are relatively heavy, potato cyst nematodes do not usually cause distinct above-ground symptoms. Affected plants often appear as having moisture or fertilizer deficiency. However, examination of roots in severely infested fields usually reveals white round immature females protruding from the roots of most plants.

Control of potato cyst nematodes usually involves a combination of procedures. Extensive surveys are carried out in the potato regions of the United States and Canada in an effort to detect potato cyst nematodes before they become plentiful or widespread. Fields where potato cyst nematodes are detected are usually taken out of potato production. Strict quarantine regulations restrict the movement of seed potatoes and soil from areas infested with potato cyst nematodes to areas which are unaffected. These regulations exist between countries and between areas in the same country. Crop rotations are a useful method of control since potato cyst nematodes do not have a wide host range. However, this method has limitations since some eggs in cysts can survive without a host for as long as 20 years. The use of nematicides has been effective in regions of the world where infestations are heavy, but the costs are high. Resistant cultivars are available and are used extensively in Europe in areas where potato cyst nematodes are widespread. Agriculture Canada has conducted a long-term evaluation of potato selections for resistance to cyst nematodes at St. John's, Newfoundland (31,32,33).

ROOT-KNOT NEMATODES

These nematodes are not a serious problem at present in the major potato areas of the world. However, certain species may cause severe damage in local situations. Root-knot nematodes (*Meloidogyne* spp.) tend to be most destructive in tropical and sub-tropical climates and are less of an economic problem in northern latitudes or in cool soil at higher elevations in warmer climates. Since potatoes are susceptible to root-knot nematodes, the trend to extending the range of potato culture into the tropics and subtropics will probably increase the seriousness of this pest in potatoes (5).

Root-knot nematodes in cooler climates are believed to overwinter primarily in the egg stage. Second-stage juveniles hatch from eggs, invade host roots and undergo a series of molts to form saccate sedentary third and fourth stage juveniles, and then adult pear-shaped females or vermiform mobile males. Each female produces 300-400 eggs in a jelly-like substance which exudes from the vulval region. Above-ground symptoms on potatoes are vague and may be mistaken for nutrient deficienty of water stress. However, roots usually develop galls or knots, and tubers may be infested when nematode populations are large.

The only root-knot species that causes problems in North America is the Columbia root-knot nematode, *Meloidogyne chitwoodi* Golden et al., 1980. This pest has been recovered from potato fields in the northwestern United States in Washington, Oregon, and Idaho where it occasionally causes significant yield reductions. The Columbia root-knot nematode is very similar to the northern root-knot nematode, *M. hapla* Chitwood, 1949, in appearance, and in the past it is likely that the former often was identified as the northern root-knot nematode.

However, recent studies have shown that the Columbia root-knot nematode differs from the northern root-knot nematode in its host and temperature preferences (10).

The most widespread root-knot species in North America is the northern root-knot nematode. Populations, however, are usually small, and damage to potatoes is not significant. Surveys conducted on Prince Edward Island (14) and in Ontario (26) indicated that northern root-knot nematodes were widely distributed, but population densities were usually too low to warrant concern. However, Olthof and Potter (24) have shown that northern root-knot nematodes can cause severe damage to potatoes in microplots. In these experiments, potato eyes (cv. Sebago) were grown in clay drainage tiles of 20 cm internal diameter and 30 cm long. Densities as low as 666 nematodes per kg of soil caused a loss of 42% in marketable yields. There were also blemishes on tubers. Therefore, the northern root-knot nematode should be regarded as a potential threat to potato production in Canada.

Root-knot nematodes are usually controlled by nematicides. Crop rotations are also quite effective in some situations even though root-knot nematode species tend to have a large host range. Resistant varieties offer much promise but they have not been used extensively (5).

POTATO ROT NEMATODE

The potato rot nematode, Ditylenchus destructor Thorne, 1945, is a serious nematode pest of potatoes in various parts of the world. It was first reported in Europe in 1857 (35). In North America the potato rot nematode was found in Idaho in 1943 (3), on Prince Edward Island in 1945 (2), in British Columbia (4) and Wisconsin (8) in 1953, and in California in 1968 (1).

The above-ground portions of the potato plant do not show any noticeable response to invasion by the potato rot nematode. Symptoms caused by this nematode are most obvious in tubers. This is the result of nematodes entering potatoes through the eyes. Small white spots develop just below the surface, and these gradually darken to greyish brown or black. Secondary organisms such as bacteria and fungi often add to the damage. The skin of the tuber is not attacked but becomes thin and cracks as underlying infected tissue dries and shrinks. Potato rot nematodes continue to live and reproduce in harvested tubers in storage, or in tubers left in the field. These nematodes can also survive on fungi or weed hosts until another potato crop is planted (5).

Control measures include healthy seed, destruction of infected plant parts in the field, elimination of weed hosts, and application of nematicides. Resistant cultivars are generally not suitable, and crop rotations are of limited value since the potato rot nematode has a wide host range. In recent years the incidence and seriousness of the pest has declined in North America, due probably to removal of infected land from production. However, this species continues to be a serious problem in eastern Europe and central Asia. To our knowledge there are no studies presently underway in Canada on the potato rot nematode.

CONCLUDING REMARKS

Suppression of plant parasitic nematodes and the diseases they cause in potatoes requires an integrated approach. Diagnostic and advisory services are a necessary prerequisite if control measures are to be utilized logically. Methods of control involve nematicides, crop rotations, tolerant or resistant cultivars, cultivation, sanitation, and quarantine regulations. To date, the most popular and effective method has been the application of nematicides. However, nematicides are expensive, and there have been isolated incidences of environmental contamination. Therefore, it is likely that other methods of nematode control in potatoes will become increasingly important.

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SEMIOCHEMICALS AND POTATO PESTS: REVIEW AND PERSPECTIVE FOR CROP PROTECTION.

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ABSTRACT

A large quantity of chemicals present in different plant or insect species influences individual insect behavior. Termed as semiochemicals, these natural chemicals have regained popularity as potential alternative methods for crop protection. The litterature concerning pheromones and allelochemicals significant for Leptinotarsa decemlineata, Macrosiphum euphorbiae, Aulacorthum solani, Aphis nasturtii, Empoasca fabae and Epitrix cucumeris is reviewed. Most of the data available relate to the mechanism of host finding and acceptance by Leptinotarsa decemlineata. The potential of using semiochemicals in crop protection has been evaluated by several authors and is reviewed.

RÉSUMÉ

Un grand nombre de substances chimiques provenant de plusieurs espèces végétales ou d'insectes, affectent le comportement individuel des insectes. Nommée substances semiochimiques, ces produits naturels ont connus un regain de popularité comme potentielles mesures de contrôle des insectes en agriculture. La littérature portant sur les phéromones et les substances allelochimiques influençant Leptinotarsa decemlineata, Macrosiphum euphorbiae, Aulacorthum solani, Aphis nasturtii, Empoasca fabae et Epitrix cucumeris est résumée. La majorité des données consernent le méchanisme de localisation et d'acceptation de la plante hôte chez Leptinotarsa decemlineata. La faisabilité d'utilisation des substances semiochimiques en protection des plantes a été évaluée par plusieurs auteurs et leur positions est résumées.

INTRODUCTION.

The potato crop is attacked by several insect pests: Leptinotarsa decemlineata (Say) (the Colorado potato beetle), Myzus persicae (Sulzer) (the green peach aphid), Macrosiphum euphorbiae (Thomas) (the potato aphid), Aulacorthum solani (Kaltenbach) (the foxglove aphid), Aphis nasturtii Kaltenbach (the buckthorn aphid), Empoasca fabae (Harris) (the potato leafhopper) and Epitrix cucumeris (Harris) (the potato flea beetle). The importance of each of these species varies with the region in Canada and the type of production (seed, transformation or fresh). However, control strategies presently used to regulate populations of these insects in potato are similar and are based on insecticide spraying.

Beside the growing concern for both environmental contamination and increasing pesticide costs, insect resistance is also becoming a problem linked to heavy insecticide use. This is especially acute in some regions of Northeastern America where the Colorado potato beetle is resistant to almost every insecticides.

A diversification in control methods seems to be the only way to effectively regulate insect populations.

The use of various control methods in an ecologically sound way is the basis of the Integrated Pest Management (IPM) concept. With the increase in popularity of IPM, more efforts have been directed toward a basic understanding of insect pests biology. Pheromones and natural products which affect insect behavior have been seriously considered as potential control methods. Such methods, based on naturally occurring products, are believed to decrease the need for insecticide applications when used within an IPM program.

Semiochemicals are molecules, produced by an organism, which after reaction with receptors produce a signal used by another organism (1). The effect of natural products on insects can be physiological, by interacting with a target site outside the sensory receptor/integrative apparatus. The term semiochemical however, is reserved for natural products which cause a behavioral change in the organism by interacting with sensory receptors which in turn alter the electrical activity in the central nervous system, and thereby change the neural directives to effector organs (58). Interactions involving semiochemicals can be between two individuals of the same species or between individuals of different species.

These reactions led to the definition of pheromone and allelochemicals (73). A pheromone is a chemical secreted by an organism to the outside that causes a specific reaction in a receiving organism of the same species. This reaction can be sexual or defensive in nature so that the chemical which triggers the reaction will be referred to as a sexual or as an alarm pheromone. An allelochemical is a chemical that is significant to organisms of a species different from its source, for reasons other than food as such. Further classification of allelochemicals can be based upon the benefit for the emitter and the receiver (allomone, kairomone etc.) or based upon the behavioral reaction. This last classification will be used herein referring to arrestant, attractant, and repellent when the chemical causes aggregation in contact with, movement toward, or movement away from the source. Stimulant and deterrent are used when the compound illicits or inhibits a certain type of behavior. The effect of a compound on an individual is not always constant nor is the effect on individuals of different species.

It is now recognized that the reaction toward pheromones and allelochemicals is influenced by several environmental factors, the population, and the physiological state of the individual. Even though progress made in the study of the role and application of semiochemicals is viewed by some as "among the most significant advances in pest control technology" (55), much more has to be done before they can play an important role in crop protection.

In the following pages, we will review the literature on the effect of semiochemicals for potato insect pests, on secondary plant products in potato and related species, and evaluate the possibility of using semiochemicals for the protection of the potato crop.

PHEROMONES AND POTATO INSECT PESTS.

Sexual pheromones.

In preliminary experiments, Wilde et al. (103) noticed that males of the Colorado potato beetle were attracted toward an air plume passing through a compartment containing females. This reaction stopped when the last two antennal segments were cut. They concluded that a sexual pheromone was present in the Colorado potato beetle. Levinson et al. (54) found that extracts from females attracted 2.3 times more males than the control, in a choice test. Extracts from males were not attractive to other males. Electroantennogram studies confirmed that male Colorado potato beetles perceive female extracts. However, a similar response, but lower in intensity, was observed using male extract and potato extract. More recently, Wiesner et al. (100) were unsuccessful in repeating the experiments of Levinson et al. (54) and found no indication of the presence of a sexual pheromone active at short distance in the Colorado potato beetle. Based on behavioral observations, Szentesi (91) found that males readily recognized the sex of another individual when contacted with the tarsi, antennae and maxillary palps. He stated that females are likely to produce a contact sex pheromone. As outlined the effects of sexual pheromone on the Colorado potato beetle are inconsistent. Whether or not sex attraction and/or recognition is based on pheromones has yet to be proven.

Sexual pheromones are known to be present in many aphid species. However, little research has been done with the potato infesting aphids.

Alarm pheromone.

It was first discovered that secretion from the cornicles of aphids produce dispersal behavior among nearby aphids (52). They demonstrated that the substance was not specific, possibly because of a differential concentration or composition between aphid species. Trans-ß-farnesene has been identified as the alarm pheromone of the green peach aphid (22). Using electrophysiological techniques, it was shown that (E) ß-farnesene was perceived by the primary rhinaria in some aphid species (104).

The presence of an alarm pheromone in the vicinity of green peach aphids causes them to walk or fall off the plants (67; 12). The proportion of aphids falling off the plant is inversely proportional to the distance from the source of pheromone (67). The sensitivity to the alarm pheromone varies with the morph and the age of the aphids (68). After a flight, alates did not respond to the alarm pheromone (33). The aphids are also more sensitive when isolated or when alates are not feeding. It takes approximatively one hour for the disturbed aphids to redistribute themselves on the plant as they were before exposure to the pheromone (12). Those reacting by walking, usually remained on the same leaves (67). Edwards et al. (22) considered that alarm pheromones could play a role in pest management. When combined with an insecticidal spray, a pheromone could enhance the spray's effectiveness by causing more movement and increasing the chance that aphids would contact the insecticide.

With the present state of knowledge dealing with pheromones in potato insect pests, control methods using pheromones can not be foreseen in the near future. Sexual pheromones of aphids seems to be the most promising for insect control using 'traditional' methods. Sexual pheromones can be used for monitoring, mass trapping, male annihilation or mating disruption (10). However, long term basic research is required before these methods can be adapted to aphid pest management. The situation is further complicated by the fact that the sexual morphs of potato infesting aphids occur on secondary hosts and that colonization of the potato crop in the spring may be the result of long range migrations. On the other hand, the reaction of aphids toward alarm pheromones varies considerably between individuals and often results in an increase in inter-plant movement. This last consequence is not desirable when limitation of the spread of potato viruses is required. At the present time and without extended research and field trials, the potential of alarm pheromones in potato crop protection can not be precisely evaluated.

ALLELOCHEMICALS AND POTATO INSECT PESTS

Host selection and acceptance.

Each phytophagous insect species has a limited host-plant range on which it can grow and reproduce. In order to maximize their reproductive potential, insects must be able to discriminate between host and non-host plants. The cues used for such discrimination can be visual, olfactory, and/or gustative in nature. The nature and intensity of the stimuli will form the host image and will vary among insect species. A large part of these stimuli are of a chemical nature. Allelochemicals are produced by plants to prevent damage by herbivores and used by insects to recognize their hosts. Host-plant recognition will depend on the nature of the plant characteristics, on the characteristics of the herbivore's sensory system, its detecting and coding capabilities, and on the central neural setting (20).

The host finding process can be divided into five steps; host-plant perception, initiation of biting, feeding action, continuous feeding, and cessation of feeding (37). Allelochemicals from plants may play a role in each step. The set of stimuli used in each step may vary in nature and/or in intensity but also between food and oviposition site locations. Since secondary plant products are often considered as protection against herbivores, we will review knowledge concerning the chemistry and physiology of these chemicals in potato and related plant species. Then, the results on the role of plant chemicals in host-plant recognition by potato insect pests will be summarized. Some results obtained with synthetic chemicals have been included when pertinent to the discussion.

Secondary plant products in potato and related species.

The genus Solanum and most members of the Solanaceae family possess a significant number of secondary metabolites that can function as deterrents against potential pests. Of these, alkaloids are the most prominent and are known to exhibit some inhibitory or toxic action against most insects. Nicotine from *Nicotiana* species and atropine from *Atropa belladonna* are neurotoxic alkaloids that affect many insects including *Leptinotarsa* species (38). Tropane alkaloids of *Datura* and *Hyoscyamus* and steroidal glycoalkaloids are likewise well-known toxic deterrents for many vertebrates and insects (43; 74; 94; 106). Extensive work has been done on the steroidal alkaloids because they are compounds of considerable scientific and commercial interest. They occur predominently as glycosides in three genera, *Solanum*, *Lycopersicon* and *Cestrum*, and have been isolated from more than 350 species (81; 88). Five main aglycone skeletons are known, all based on a C_{27} cholestane structure but the solanidane and spirosolane-types have been researched more fully. A number of these glycoalkaloids have been tested for activity and the relationship between repellency and molecular structure has been at least partly established (34).

In addition to alkaloids, members of the Solanaceae also synthesize many other secondary plant metabolites that perform a defensive role. Nicandrenone, a steroid from *Nicandra physalodes*, is a potent deterrent to the tobacco hornworm, *Manduca sexta* (71) and the Colorado potato beetle (40). The ketohydrocarbon 2-tridecanone from *Lycopersicon hirsutum* is toxic to a number of arthropod pests (48). Two *Withania* steroids, withanolides and withaferims as well as nicandrenone and nicalbins, have been reported as antifeedants for insects (3; 4).

In tomatoes, the phenolic compounds such as chlorogenic acid and rutin, are growth inhibitors to the fruitworm (23; 42).

Another specialized type of chemical defense involves plants that utilize mucilages from glandular trichomes on the aerial surfaces to entrap or otherwise impede arthropod pests. In the genus *Solanum*, two distinct types of glandular trichomes predominate and they are atypical of the other solanaceous genera (87). Normally, the multicellular or type A glandular trichomes consist of short stalks with tetralobulate glandular tips. When ruptured, the glands release a clear water soluble material wich on contact with atmospheric oxygen hardens into a dark insoluble substance (30). The other or type B trichomes are long slender hairs with unicellular glandular tips. These glands freely exude a durable sticky material. Although their presence is detectable in cultivars of *S. tuberosum* the tetralobulate of type A glandular trichomes are known to occur abundantly on the wild potato species, *S. berthaultii*, *S. polydenium*, *S. tarijense*, *S. neocardenassi* and the tomato *Lycopersicon esculentum*. In some accessions of *S. berthaultii* and *S. neocardenassi* both types of trichomes appear to effectively work in concert against insects (96; 53).

Indications of phenolic oxidase activity in the type A trichomes of *S. berthaultii* were initially reported by Gibson (30). Polyphenoloxidase and peroxidase activities were later confirmed (32; 83). Evidence for the presence of phenolic substrates such as chlorogenic acid (in *S. polyadenium*) and esters of p-hydroxyphenylpropionic acid (in *S. berthaultii*) have since been reported (5). Gc-ms of the exudate from the type B trichomes of *S. berthaultii* yielded evidence for the presence of various sesquiterpenes including the aphid alarm pheromone (E)-β-farnesene (31). Further detailed chemical analysis by King et al. (49; 50; 51) demonstrated that the sticky exudate from the type B trichomes of both *S. berthaultii* and *S. neocardenassi* is composed primarily of sucrose fatty acid esters. Preliminary investigations indicate that the type B trichome exudate of other Solanaceae genera also consists predominantly of sucrose or glucose fatty acid esters. Utilization of mucilages by pubescent members of the Solanaceae family in some respect resembles the trapping of insects by certain carnivorous plants. Furthermore, sucrose fatty acid esters with the appropriate substitution pattern, i.e. C-2, C-4 or C-1' are bitter tasting (36). Interestingly, all the type B trichome sucrose fatty acid esters characterized to date are substituted in at least one of the positions required for bitterness.

Host selection in Colorado potato beetle.

In wind tunnel situations, adults of the Colorado potato beetle demonstrate an anemotactic reaction. This reaction can be enhanced by starvation (fed beetles do not respond) (57). No differences between male and female were noted. When the last four antennal segments are cut, the anemotactic response stops. Plant odor incorporated into the air plume enhances, reduces, or does not affect up-wind movement, depending on the plant species used (Table 1) (57; 102; 103). Beetles having fed for two hours and then starved are more attracted toward potato odor than unexperienced beetles (99). In general, the odor of host plant species or related species will increase the anemotactic response. The movement is more rapid, direct to the source, and with less turn than without odor (98). Wilde (102) observed that potato odor may act as an arrestant for flying beetles in a field situation.

The potato odor is composed of several compounds perceived by the Colorado potato beetle (Table 2). None of these are attractive by themselves (57). The addition of one of the components to potato odor decreases the attractiveness. Potato odor perception is based on an exact ratio of several compounds not specific to Solanaceous plants (57). The presence of other plant species in the vicinity of the

Table 1.- effect of various plant species on the host acceptance, growth and attraction of larvae and adult colorado potato beetles.

Plant species	Larvae			Adult	
	accep.[1]	growth[1]	wt gain[2]	accep.[3]	attrac.[4]
Aceraceae					
Acer saccharinum	--	--	--		
Amaranthaceae					
Amaranthus ascendens				-	
Amaranthus graecizans	--	--			
Amaranthus retroflexus	--	--	--	-	
Gomphrena globosa				-	
Apocynaceae					
Apocynum cannabinum	--	--	--	-	
Araliaceae					
Hedera helix	--	--	--		
Asclepiadaceae					
Ampelamus albidus	++	+	+		
Asclepias incarnata	--	--	-		
Asclepias sullivantii	--	--	+		
Asclepias syriaca	+++	+++	++	+++	
Asclepias tuberosum	++	++			
Asclepias verticillata	--	--	+		
Caesalpiniaceae					
Cercis canadensis	--	--	--		
Gleditsia triacanthos	--	--	-		
Pisum sativum	+	++			
Cannaceae					
Canna indica				-	
Caprifoliaceae					
Lonicera japonica	--	--	--		
Caryophyllaceae					
Saponaria officinalis				-	
Chenopodiaceae					
Beta vulgaris	--	--	--	-	
Chenopodium album	--	--	--	+	
Chenopodium hybridum				+	
Spinacia oleracea	--	--			
Compositae					
Achillea millefolium	--	--			
Ambrosia trifida	--	--	--		
Anthemis cotula	--	--			
Arctium minus	--	--		-	
Arctium tomentosum				-	
Artemisia stellariana	--	--			
Artemisia vulgaris				-	
Centaurea pannonica				-	
Chrysanthemum indicum				-	
Cichorium intybus	+	+		-	
Circium arvense				-	
Circium vulgare	+++	++	++		
Dahlia pinnata				-	
Doronicum pardalianches					0
Erigeron strigosus	--	--			
Eupatorium rugosum	+	+			
Galinsoga parviflora	+	++		+++	
Helianthus annuus	--	--	-	-	
Lactuca sativa				++	
Lactuca sativa var. capitata	++	++	+		
Lactuca sativa var. romana	++	+++	++		
Lactuca scariola	+	++	++		
Onopordum acanthium				-	
Senicio vulgaris				-	
Solidago virgo-aurea				-	
Sonchus oleraceus	+	+		++	
Taraxacum officinalis	--	--	0		-
Zinnia elegans				-	
Convolvulaceae					
Calystegia sepium				-	
Concolvulus americanus	--	--	--		

Table 1.- Continued.

Plant species	Larvae			Adult	
	accep.[1]	growth[1]	wt gain[2]	accep.[3]	attrac.[4]
Convolvulus arvensis				-	
Ipomoea hederacea	--	--	--		
Corylaceae					
Alnus incana					0
Cruciferae					
Brassica napus var. arvensis				++	
Brassica nigra	--	--			
Brassica oleracea var. capitata	++	+	+	+	0
Brassica oleracea var. cauliflora				++	
Brassica pekinensis					0
Capsella bursa-pastoris	++	++	++		
Lepidium virginicum	--	--	--		
Raphanus sativus	+	--	-	-	0
Sinapis arvensis				-	
Thlaspi arvense	+	--			
Cucurbitaceae					
Citrillus vulgaris	--	--	0		
Cucumis sativus				-	
Cucurbita pepo	--	--	--		
Euphorbiaceae					
Euphorbia corollata	--	--	--		
Euphorbia helioscopia				-	
Fagaceae					
Quercus alba	--	--	--		
Ginkgoaceae					
Ginkgo biloba	--	--	--		
Gramineae					
Adropogon ischaemum				-	
Echinochloa crus-galli				-	
Poa annua					-
Poa pratensis	--	--	-		
Secale cereale	--	--			
Zea mays	--	--	-	-	
Hamamelidaceae					
Liquidambar stryaciflua	--	--	--		
Juglandaceae					
Carya ovata	--	--	--		
Labiatae					
Mentha piperita				-	
Salvia pratensis				-	
Salvia splendens				-	
Salvia verticillata				-	
Leguminosae					
Glycine soja	--	--	--		
Medicago sativa				-	0
Melilotus albus				-	
Phaseolus lunatus	--	--	0		
Phaseolus vulgaris var. nanus				++	0
Pisum sativum spp. hortense				+++	0
Robinia pseudo-acacia				-	
Trifolium arvense				+	
Trifolium pratense	--	--	-		
Liliaceae					
Allium cepa				+++	
Asparagus officinalis	--	--	--		
Polygonatum biflorum	--	--	--		
Malvaceae					
Abutilon theophrasti	--	--	-		
Malva neglecta	--	--			
Malva silvestris				++	
Moraceae					
Maclura aurantiaca				+	
Maclura pomifera	--	--	--		
Morus alba	+	--	+		

Table 1.- Continued.

Plant species	Larvae accep.[1]	Larvae growth[1]	Larvae wt gain[2]	Adult accep.[3]	Adult attrac.[4]
Oleaceae					
Fraxinus americana	--	--	--		
Syringa vulgaris				-	
Papaveraceae					
Papaver somniferum				+	
Phytolaccaceae					
Phytolacca americana	+	--	--		
Pinaceae					
Pinus strobus	--	--	--		
Tsuga canadensis	--	--	--		
Plantaginaceae					
Plantago lanceolata	--	--		-	
Plantago major				-	
Plantago rugelii	--	--	--		
Platanaceae					
Platanus occidentalis	--	--	--		
Polygonaceae					
Polygonum lapathifolium				-	
Polygonum persicaria	--	--	--		
Rheum undulatum				-	
Rumex acetosa				+	
Polypodiaceae					
Adiantum pedatum	--	--	--		
Athyrium pycnocarpon	--	--	-		
Cystopteris bulbifera	--	--	--		
Dryopteris marginalis	--	--	--		
Polystichum acrostichoides	--	--	--		
Portulacaceae					
Portulaca oleracea	--	--	-		
Ranunculaceae					
Clematis vitalba				-	
Ranunculus acer				+	
Rosaceae					
Fragaria ananassa				-	
Malus pumila				-	
Prunus armeniaca var. communis				-	
Prunus domestica var. hungarica				+	
Prunus serotina	--	--	-		
Pyrus communis	--	--	-		
Rosa centifolia				-	
Rubus sp.				-	
Salicaceae					
Salix babylonica	--	--	--		
Scrophulariaceae					
Antirrhinum majus				-	
Verbascum phlomoides				-	
Veronica agrestis				-	
Scrophulariaceae					
Verbascum thapsus	+	--	-		
Simaroubaceae					
Ailanthus glandulosa				-	
Solanaceae					
Capsicum annuum	++	+	+	+	+
Datura metaloides	+	--	-		
Datura stramonium	++	+	-	++	+
Hyoscyamus niger					+
Lycium halimifolium	+	++	+		
Lycopersicon esculentum	+++	+++	+		
Nicandra physaloides	+	--	--	-	
Nicotiana rustica	++	--	--		
Nicotiana tabacum	++	--	--	+	+
Petunia atkinsiana				-	
Petunia hybrida	+++	+	++		+
Physalis heterophylla	+++	+	0		
Physalis subglabrata	+	--	-		

Table 1.- Continued.

Plant species	Larvae accep.[1]	Larvae growth[1]	Larvae wt gain[2]	Adult accep.[3]	Adult attrac.[4]
Solanum aviculare				++++	
Solanum carolinense	+++	+++	++		+
Solanum demissum					+
Solanum dulcamara	+++	+++	++		+
Solanum esculentum					+
Solanum luteum					+
Solanum lycopersicum				++	+
Solanum melongena	+++	+++	++	++++	
Solanum nigrum	++	--	+	++	+
Solanum rostratum	+++	+++	++		
Solanum tuberosum	+++	+++	++	+++	+
Taxaceae					
Taxus canadensis	--	--	--		
Tiliaceae					
Tilia americana	--	--	--		
Tropaeolaceae					
Tropaeolum majus					+
Umbelliferae					
Apium graveolens	--	--			+
Daucus carota	--	--			
Pastinaca sativa	--	--	-		
Petroselinum crispum	--	--	--		
Urticaceae					
Urtica dioica				+	
Urtica urens				+	
Violaceae					
Viola sp.	--	--	--		
Vitaceae				-	
Parthenocissus inserta					
Vitis aestivalis	--	--	--		
Vitis vinifera				-	

[1] Data from Hsiao and Fraenkel (1968c), acceptability and growth on fresh leaves. -- = negative, +++ = highly positive.

[2] Data from Hsiao and Fraenkel (1968 b), weight gain on art. diet supplemented with leaf powder. Scale as [1].

[3] Data from Jermy (1961), acceptability of leaf disk in sandwich choice test. - = 0-5% of control, + = 6-25%, ++ = 26-75%, +++ = 76-110% and ++++ = more than 110%.

[4] Data from Visser and Nielson (1977) and Wilde de et al. (1969), attractiveness of plant odour. - = repellent, o = neutral and + = attractive.

potato plants can mask the potato odor by changing this ratio. Inter-planting potato with tansy or catnip can reduce Colorado potato beetle population by 60 to 100% (75). In laboratory experiments, Thiery and Visser (99) were able to neutralize the beetle's orientation response toward potato odor by adding wild tomato or cabbage odor. The role of plant odor in host finding (and possibly in host acceptance as hypothesized by Wilde (102)) can not be denied but the turbulent character of the wind in the field reduces its precision (98). Olfactory orientation should be seen as the first step in host finding by the Colorado potato beetle.

It has long been thought that the host specificity of the Colorado potato beetle was only related to the presence of phagostimulants specific to some Solanaceous species. Hsiao and Fraenkel (39) established that sucrose, chlorogenic acid, and phospholipids from potato leaves were phagostimulants while some organic acids were not (Table 3). They found a fraction of potato leaves extract, highly stimulative and tentatively identified the compound as a phenolic flavonoid. In artificial diets, the effects of feeding stimulants are further accentuated by inorganic salts (KCl, KH_2PO_4, NaCl) which serve as feeding co-factors with additive or synergistic effects (37).

Electrophysiological experiments with Colorado potato beetle larvae revealed the presence of chemoreceptors on the galea, maxillary palps, and labial palps that were stimulated by sodium chloride, sucrose, gamma-aminobutyric acid, alanine, alpha-aminobutyric acid, serine and proline (59; 62). The receptivity was correlated with behavioral results on the phagostimulatory effect of these compounds. In the adult, receptors specific to amino acids were found on the galea and they responded mainly to L-alanine and gamma-aminobutyric acid (61). It is then possible that quantitative or qualitative differences in the amino acid composition among plant species can be used by the Colorado potato beetle as cues for host selection (59).

Another way an insect can recognize its hosts is by being sensitive to allelochemicals present in non-host plants. These compounds will then act as repellents or feeding deterrents for the insect. In that regard, the more specialized an oligophagous insect, the more its chemosensory system should be sensitive to deterrents. The Colorado potato beetle being restricted to only a few plant species, should be sensitive to many different compounds (92).

Hsiao and Fraenkel (41) found that most plants are not eaten by 4th instar larvae and contain feeding deterrents or toxic compounds (40) (Table 1). They found that only a few non-host plant species can support Colorado potato beetle growth. *Asclepias syriaca*, *Lactuca sativa* var. romana can be used as food by the Colorado potato beetle for several generations and *Asclepias tuberosa* and *Capsella bursa-pastoris* for one generation. In choice tests with potato plants, these plant species were not preferred and most of the time not defoliated. Similar results were gathered by Jermy (44) with adults using sandwich tests (Table 1). They concluded that most plants contain feeding deterrent(s) and that the restriction of the Colorado potato beetle to Solanaceous species is maintained by the absence of such feeding inhibitors (40) and the sensitivity of the Colorado potato beetle to non-host feeding deterrents (45). This conclusion is also supported by the fact that 3rd instar larvae will feed more on non-host plants when the palps are cut (101). Trials to isolate the active feeding deterrents by fractionation indicated that the active chemical(s) vary in nature among plant species (40). Tests with pure compounds from plant origin show that products of the same chemical class, differ in their anti-feedant activity (Table 2) (47).

In accordance with the results mentioned above, Benepal and Martin (8) noticed that in fields where weeds were not controlled, *Datura stramonium* was used as alternate host while *Polygonum pensylvanicum*, *Amaranthus retroflexus*,

Table 2.- EAG responses of Colorado potato beetle to test compounds (10^{-3} M in Paraffin oil v/v) as a percent of the response to cis-3-hexen-1-ol[1].

Compounds	Response
Propionic acid	0
Butanoic acid	0
Pentanoic acid	0
Hexanoic acid	0
Heptanoic acid	0
Linoleic acid	0
Hexanal	21
1-Hexanol	94
2-Hexanol	17
3-Hexanol	33
trans-2-Hexenal	39
trans-2-hexen-1-ol	146
cis-2-Hexen-1-ol	75
cis-3-Hexen-1-ol	100
trans-3-Hexen-1-ol	101
cis-3-Hexenylacetate	69
2-Methylbutanol-1	0
3-Methylbutanol-1	1
1-Penten-3-ol	6
5-Hexen-1-ol	37
1-Octen-3-ol	57
Butylacetate	1
Benzylacetate	7
Benzaldehyde	5
Salicylaldehyde	6
Methylsalicylate	22
Eugenol	9
Δ-Carene	0
(+)-Limonene	0
alpha-Pinene	0
β-Ionone	0
Geraniol	0
Nerol	0
Linalool	18
Citronellol	4
2-(Methylthio)ethanol	2
3-(Methylthio)propanal	4
2-Pentanone	6
6-Methyl-5-Hepten-2-one	7
2-Hendecanone	1
Pyridine	6

[1] From May and Ahmad (1983).

and Ambrosia artemisiifolia were not. Solanum berthaultii decreases the survival rate to 2% compared to 41% on potatoes (105), as a result of starvation of young larvae. The survival rate of adults is similar on both plant species (15). The mechanism of resistance against the Colorado potato beetle is presently under investigation by the senior author and preliminary results demonstrate the presence of feeding deterrent(s) at the surface of the leaves.

The nature and magnitude of the effect of glycoalkaloids vary with the compound and the life stage of the Colorado potato beetle (21; 88). Copper containing fungicides, such as Bordeaux mixture, reduce feeding by the Colorado potato beetle (16). When copper hydroxide was used in field trials, the defoliation was reduced by 44 to 100% during the entire season (33). Similar results were obtained with Bordeaux mixture (90), copper oxychloride, and Brestan (70). Copper sulfate is also an effective feeding deterrent but sodium sulfate has no effect on both larvae or adult Colorado potato beetles (16). Tannin is a strong anti-feedant and is more effective on young larvae (76). Weak to strong feeding inhibition have been observed with tertiary amides and their quartenary ammonium derivatives (19).

As seen (Table 3), a large number of chemicals are known as anti-feedants for the Colorado potato beetle. However, no common chemical structure explaining the similarity of the reaction has been so far recognized (92). Using diversely substituted butadienes, Muckensturn et al. (69) reported that the steric factor is of prime importance in correlation to anti-feeding activity and that the Colorado potato beetle is more sensitive to lipophilic hydrocarbons. A series of alkyl-aryl-ethers were also tested by Matolcsy et al. (56). They found that feeding inhibition was enhanced by a substitution on the aromatic ring and specially when an halogen was substituted in this position. Electrophysiological techniques also helped to elucidate the mode of action of feeding deterrents. It was demonstrated that glycoalkaloids act on chemoreceptors by damaging the cells and by doing so, inhibit the perception of phagostimulants (61).

Volatile compounds present in the vicinity of the plant can prevent feeding by the Colorado potato beetle (75). Tansy oil and several of its components reduce feeding activity when introduced in an air flow directed toward potato leaves. However, Jermy et al. (47) found that essential oil of several plant species did not prevent feeding by 3th instar larvae when applied on potato leaflets.

In choice tests with S. tuberosum, S. nigrum received around 20% more eggs (41). S. nigrum is acceptable (some feeding observed) for larvae but does not support growth. The authors concluded that oviposition is driven by a set of cues different from the one used for host finding. The same phenomenon has been reported with S. luteum (37). Under lab conditions, a few non-solanaceous plants also attract a higher amount of egg-deposition than on neutral substrates (37). Oviposition preference, therefore, is not a mere consequence of feeding preference and is based upon several stimuli not specific to Solanaceous plants (37). Szentesi (90) also reported that potato fields sprayed with Bordeaux mixture (a known feeding deterrent) received more eggs than untreated plots but the opposite response was obtained in the laboratory by Chapman (16). Also, treatments with copper oxychloride resulted in a decrease in oviposition, the adults leaving the field (70).

A fair amount of data has been accumulated on the host finding of the Colorado potato beetle. The relative importance of each of these results at each steps of the host selection have not been integrated into a comprehensive model. The main contribution is the use of anti-feedant fungicides to protect potato plants during the entire summer. This indicates that the use of feeding deterrent for controlling the Colorado potato beetle is possible.

Table 3.- Feeding response of the Colorado potato beetle to various chemicals.

Chemicals	Feeding
Bordeaux mixture 1,2	--
Copper sulfate 2	--
Potassium sulfate 10	--
Sodium sulfate 2	0
Sodium chloride 10	--
Potassium chloride 10	--
Copper oxychloride 3	--
Leptine 4	--
Tomatine 4,5	--
Demissine 4	--
Solanine 4,10	0
Chaconine 4	0
Cucurbitacine D 6	--
Coumarin 6	0
Scopoletin 6	0
Isoscopoletin 6	0
Esculetin 6	0
6,7-dimethoxycoumarin 6	0
Nicotine 7	--
Physostigmine 7	--
Colchicine 7	--
Veratrine 7	--
Aconotine 7	--
Delphinime 7	--
Cantharidin 7	--
Quassiin 7	--
Picrotorin 7	--
Tanin 8	--
Alpha-pinene 9	++
dl-alpha-pinene 9	0
Alpha-terpinene 9	--
Gamma-terpinene 9	--
Cineole 9	--
Cymene 9	--
Alpha,β-thujone 9	--
Camphor 9	0
Terpinen-4-ol 9	--
Dihydrocarvone 9	--
Carvone 9	--
Borneol 9	0
Sucrose 7,11,10	++
Glucose 7,10	++
Fructose 7,10	++
Melezitose 7	++
Mannose 7	0
Maltose 7	0
Turanose 7	0
Gamma aminobutyric acid 7,12,10	++
Alpha-aminobutyric acid 7,10	++
β-aminobutyric acid 7	++
Alanine 7,10	++
Serine 7	++
Proline 7,10	++
Glutamic acid 10	++

Chemicals	Feeding
Glycine 10	++
Aspartic acid 10	++
Chlorogenic acid 11	++
Quinic acid 11	0
Caffeic acid 11	0
Ferulic acid 11	0
β-coumaric acid 11	0
Phospholipids (potato) 11	++
Stearic acid 10	++
Palmitic acid 10	++
Oleic acid 10	++
Oxalic acid 10	--
Steroids 7	0
Cholesterol 10	0
Stigmasterol 10	0
β-sitosterol 10	0
Cycloartenol 10	0
B vitamins 7	0
Lecithin 7	++
Phosphatidyl L-serine 7	++
Inositol phosphatide 7	++
Phenolic flavonoid ? 11	++
Butadiynes-1-3 (22 compds) 13	0 to --
Ammonium salts 14	0 to --
4-chlorophenoxy-ethanol 15	--
2,4,6 trichlorophenyl-methyl-ether 15	--
2,4,6 trichlorophenoxy-ethanol 15	--
2,4,6, trichlorophenoxy-acetic acid 15	--
Alpha(2,4,6 trichlorophenoxy)-proprionic acid 15	--
2,4,6 tribromophenoxy-ethanol 15	--
4-methoxyphenoxy-ethanol 15	0
3,5 dichlorophenoxy acetic acid 15	0
3,5 dichlorophenoxy acetamide 15	0
3,5 dichlorophenoxy-N-diethyl 15 acetamide 15	0

1 Szentesi, 1981.
2 Chapman, 1974.
3 Murbeck and Corbaz, 1963.
4 Demock and Tingey, 1985.
5 Koch, 1970.
6 Jermy et al., 1981.
7 Hsiao, 1969.
8 Pospisil, 1982.
9 Panasiuk, 1984.
10 Ritter, 1967.
11 Hsiao and Fraenkel, 1968.
12 Mitchell, 1974.
13 Muckensturn, 1986.
14 Darwish and Matolcsy, 1981.
15 Matolcsy et al., 1968.

Host selection in Potato infesting aphids

Bromley and Anderson (11) studied the olfaction of *Dasonovia ribis-nigri* using electrophysiological techniques. The primary rhinaria were sensitive to many compounds and often showed an antagonistic reaction (mainly to terpenes). These authors hypothesized that olfaction may play a role in host selection by aphids. However, the role of olfaction in host finding for potato infesting aphids has not yet been evaluated.

It has been suggested that the final selection of a host by aphids is favored by the same characteristics that favor subsequent aphid multiplication (25). Differences in the resistance level of *Solanum* species (29, 77; 78) (Table 4) and potato varieties (2) to potato infesting aphids were observed. This can be a consequence of differences in the host selection mechanism and/or the primary nutritional requirement of these aphids. The host selection mechanism in the green peach aphid is based on the absence of deterrent (85). The host acceptance by aphids is primarily based on the nutritionnal value, but secondary compounds play a minor role (24). Mittler and Dadd (65) note that the probing duration of the green peach aphid was longer on diets containing phagostimulants (sucrose and amino acids). The stronger the phagostimulative effect of the diet, the deeper the stylets were inserted. When a more complete diet was used, the stylets insertion was shallow. They concluded that phagostimulants act as arrestants and prolong the stylets insertion period while a complex diet, resembling the sap, inhibits stylets penetration. Host selection and guidance of the stylets is probably based on chemical cues. When in the diet, sucrose and amino acids (25) produce an increase in probing duration (24; 65) and diet uptake (63). It is interesting to note that the preference for amino acid containing diets, was observed only when sucrose was also present. The synergistic effect of amino acid on sucrose is however not explained yet (63; 65). The growth rate of the green peach aphid has been correlated with asparagine and glutamide, methionine, and leucine concentration in *Brassica* plants in the field (24) The growth rate phenomenon was also correlated with asparagine, glutamine, glutamic acid, proline, and phenylalanine concentration in potted plants grown in greenhouses (26). Using an artificial diet, methionine was found to be the amino acid stimulating feeding the most. It was followed by cysteine and histidine (64). The other amino acids were considered as phagostimulants but to a lesser degree or only in mixture. A low concentration of sinigrin stimulated the feeding and reproduction responses of the green peach aphid but had opposite effects on the foxglove aphid (72).

Recent findings by Campbell et al. (13) showed that the plant matrix polysaccharide may be the phagostimulant that initiates probing and keep stylets penetration going. The green peach aphid was differentially stimulated by several monosaccharides or plant matrix polysaccharides incorporated into an agar layer, deposited over a diet sachet. Some compounds were deterrents and prevented feeding by the green peach aphid (Table 5). The authors suggested that sensitivity to plant matrix polysaccharides may be the main host selection mechanism in aphids. However, Montgomery and Arn (66), using two layer diet sachets, found that the presence of feeding deterrents in the first layer did not prevent further penetration and feeding in the second layer by the green peach aphid. This supports Feeny's (28) view that a repellent or a deterrent has to be backed by the presence of a toxic effect in order to protect the plant by preventing the rapid evolution of insect genotypes able to attack it.

By painting the juice of resistant *Chrysantemum* varieties on the leaves of susceptible one, immunity to the green peach aphid can be transferred. It is to be expected that the resistance to aphids of some cultivars should result from deterrent compounds (25). Several chemicals were tested for feeding deterrence

Table 4.- Relative resistance of Solanum species against the potato flea beetle, the potato leaf hopper, the potato aphid and the green peach aphid.

Solanum spp.	Flea beetle			Leafhopper			Potato aphid			Green peach aphid		
	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3
acaule	98.3	59.0	3	7.9	9.5	9	87.0	53.3	29	155.5	81.1	31
acroscopicum				4.0	--	1	68.5	6.4	2	113.3	79.3	3
agrimonifolium				0.0	--	1	132.0	81.3	7	204.5	90.0	6
ajanhuiri	74.0	--	1	25.5	15.3	2	93.4	36.5	5	85.5	42.2	4
andreanum							22.7	19.0	3	29.5	0.7	2
berthaultii				0.0	--	2	176.2	152.0	5	217.8	233.4	5
boliviense	28.0	--	1	15.0	--	1	105.2	56.2	5	47.0	15.0	6
brachistotrichum				0.0	--	2	75.0	34.7	4	5.3	2.7	6
brachycarpum	23.0	--	1	0.0	--	1	71.6	68.1	5	148.3	63.7	4
brevicaule	77.5	23.3	2	8.0	--	1	138.4	45.9	5	98.5	145.7	4
brevidens							124.8	48.6	4	81.5	17.7	2
bukasovii	151.5	90.9	2	3.3	4.0	3	57.3	57.3	6	26.2	21.6	6
bulbocastanum	40.8	38.8	5	4.3	7.3	13	48.2	34.0	42	16.4	17.6	37
canasense	64.5	31.1	4	1.0	1.4	4	50.9	15.7	15	29.3	30.7	16
cardiophyllum				6.0	8.4	2	72.6	30.7	5	23.6	25.5	10
chacoense	95.3	28.6	4	3.8	7.6	4	173.6	91.1	23	204.4	93.7	21
chaucha							141.5	89.8	2	155.0	--	1
chiquidenum							64.0	--	1	29.5	21.9	2
chomatophilum				0.0	--	1	68.5	44.9	6	14.4	8.4	5
colombianum							237.0	192.3	2	175.5	3.2	2
commersonii	44.0	--	1	7.0	--	1	123.0	87.7	2	97.5	36.1	2
curtilobum				18.8	9.4	4	82.0	38.8	6	88.0	50.3	9
demissum	56.4	22.6	5	2.4	4.6	9	83.0	84.0	33	178.3	123.0	33
ehrenbergii	42.0	--	1	2.6	3.4	10	80.9	35.4	18	21.6	20.5	19
etuberosum							86.3	35.3	3	13.5	0.7	2
fendleri	93.4	46.7	7	11.1	12.2	8	122.8	85.3	25	65.6	49.2	25
gourlayi	81.0	--	1	0.0	--	1	76.0	31.9	6	42.5	40.1	4
guerreroense	137.0	--	1	0.0	--	1	56.7	7.6	3	171.0	89.1	2
hjertingii	112.8	20.6	4	7.6	6.8	5	30.7	20.2	15	25.2	19.1	13
hougasii	77.0	--	1	0.0	--	1	73.7	58.5	6	95.3	65.7	4
huancabambense	152.0	--	1				122.0	77.8	2	28.0	--	1
infundibuliforme	59.0	--	1	82.0	--	1	65.5	9.2	2	45.5	64.3	2
jamesii	81.0	--	1	1.3	1.4	3	156.4	81.5	9	27.8	19.7	13
kurtzianum				0.0	--	1	246.0	123.0	7	303.7	126.6	6
leptophyes							544.0	--	1	84.0	--	1
maglia				0.0	--	1	177.0	--	1	291.5	190.2	2
marinasense	96.0	--	1	1.0	--	1	95.0	42.0	3	31.8	41.0	4
medians	43.0	--	1	0.0	--	2	65.2	35.8	5	100.5	69.1	4
megistacrolobum	31.7	10.6	3	5.0	7.2	8	111.0	144.0	18	53.0	42.4	21

Table 4.- Continued.

Solanum spp.	Flea beetle			Leafhopper			Potato aphid			Green peach aphid		
	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3	Mean^2	St. dev.	n^3
michoacanum	72.0	19.8	4	3.2	4.8	6	58.2	13.2	9	5.5	6.0	10
mochiense							197.0	--	1	172.0	--	1
moscopanum	98.0	--	1				65.0	21.2	2	56.0	--	1
multidissectum	96.7	51.0	3	1.2	1.6	6	39.8	25.4	19	27.2	20.1	20
oplocense							233.0	--	1	103.0	--	1
oxycarpum	99.0	--	1				65.3	75.9	6	105.0	21.0	2
pampasense	17.0	--	1	0.0	--	2	89.8	47.8	4	81.0	67.4	5
papita	42.5	23.3	2	11.8	5.9	4	109.3	56.3	9	96.5	43.8	10
phureja	92.0	--	1	22.6	13.6	16	86.1	45.3	26	70.4	49.1	39
pinnatisectum	80.3	24.1	3	0.0	--	3	179.2	95.2	13	94.9	37.0	13
polyadenium	41.5	45.9	4	0.0	--	2	166.5	119.6	13	157.3	94.6	8
polytrichon	46.8	16.6	8	0.7	1.2	9	44.9	39.3	29	75.9	78.2	24
raphanifolium	59.0	14.1	2	7.0	3.5	3	75.5	40.2	11	95.8	70.4	9
sambucinum				0.0	--	1	101.5	17.7	2	166.0	86.3	2
sanctae-rosae	52.7	41.5	3	11.4	8.0	5	104.8	28.7	6	12.1	7.9	15
simplicifolium				21.8	6.5	4	131.3	58.1	8	201.6	84.6	13
soukupii				0.0	--	1	76.0	4.2	2			
sparsipilum	138.0	--	1	13.0	--	1	230.1	113.5	8	187.6	106.1	9
spegazzini	57.0	26.9	2	0.0	--	2	91.5	48.1	4	41.3	25.9	4
stenophyllidium	9.0	--	1	1.0	1.4	2	81.4	39.0	7	2.8	3.4	10
stenotomum	153.0	--	1	15.4	18.5	9	89.8	44.4	20	90.2	58.8	22
stoloniferum	70.3	42.2	16	9.6	6.7	19	44.9	34.2	49	32.4	34.1	46
sucrense				5.3	9.0	3	170.3	114.9	4	201.2	147.5	5
tarijense	45.0	--	1				256.2	127.8	6	161.8	122.6	5
tuberosum subsp. tuberosum	71.0	24.5	3	18.3	12.8	110	76.1	41.6	45	82.0	72.1	126
tuberosum subsp. andigena	98.3	59.0	3	23.7	14.2	33	79.9	48.5	44	82.5	69.8	57
vallis-mexici							36.0	--	1	21.0	--	1
venturii				19.0	--	1	82.0	--	1	29.5	4.9	2
vernei	33.5	6.4	2	24.0	--	1	155.3	79.4	3	153.3	72.7	3
verrucosum	86.0	41.7	11	5.5	6.1	8	59.6	39.6	21	55.5	45.7	19

[1] Data from Radcliffe and Lauer (1967, 1968, 1970) and Ephraim and Radcliffe (1968).

[2] Relative resistance defined as percent of # of insects on Solanum spp./# of insects on S. tuberosum var. Red Pontiac.

[3] Number of accession tested

with the green peach aphid but only sinigrin and tomatine were active in a choice test (Table 5). In no-choice situation, several compounds reduced survival (85). A decrease in the growth rate of the green peach aphid has been correlated with the concentration in gamma-aminobutyric acid, tyrosine and proline in Brassica plants (24; 26).

Based on the results presented above, it seems that host selection by aphids is not only based upon nutritionnal considerations. Olfaction may play an important role but results for the potato infesting aphids are not available. The importance of the color in long to mid-range orientation toward plants is well established. The color is also implicated in the initiation of the probing behavior in the green peach aphid and the potato aphid (Pelletier, unpublished data). Phagostimulants (mainly sugars) and the absence of feeding deterrent stimulate stylets penetration until the phloem is reached. The inhibition of stylets penetration and stimulation of feeding are probably a consequence of a change in the concentration or composition of feeding stimulants (possibly the presence of amino acids).

Data on the mechanism of host selection in potato infesting aphids are available only for the green peach aphid. Similar research will have to be conducted with the other aphid species. It is also important to determine the effect of allelochemicals on each step of the host selection mechanism for these aphids.

Host selection in potato leafhopper and potato flea beetle.

Leafhoppers can detect chemical cues when probing by pulling fluids up their stylets to the precibarium, where chemosensilla monitor chemical constituents. The chemical stimuli involved are however, barely understood (6).

Some sugars such as glucose, sucrose, and lactose increase feeding by the potato leafhopper (18). Chemical resistance of the potato against the potato leafhopper is provided by the presence of glycoalkaloids which decrease the duration of the salivation-ingestion activity (80; 95). Tomatine, solanidine and to a lesser degree, solanine, and demissidine reduce feeding in the potato leafhopper while tomatidine has no effect (17). In high concentrations (more than 400mM), fructose, trehalose, and raffinose also decrease feeding by the potato leafhopper (18).

Data on the mechanism of host selection in the potato leafhopper are insufficient and totally lacking for the potato flea beetle. Almost everything has to be done with these insects before the use of allelochemicals in control programs can be implemented. Based on the resistance of Solanum species (Table 4), the mechanism of host selection of these insects differs greatly.

PROSPECT FOR THE USE OF SEMIOCHEMICALS IN POTATO CROP PROTECTION.

The possibility of using semiochemicals for crop protection has long been recognized and is regaining popularity (1; 7; 9; 10; 16; 20; 28; 45; 55; 58; 84; 89). Even if the method can provide considerable advantages, enthusiasm has to be tempered and difficulties recognized.

One of these constraints is the requirement for basic (perhaps long-term) studies on the biology of the target pest(s) and the need for intensive evaluation in large-scale field trials (55). This should also include an evaluation of the consequences for the various species interacting with the target insect in the agroecosystem. Lewis (55) stated that our main constraint is that "the period of

Table 5.- Feeding response of the green peach aphid to various chemicals.

Chemicals	Feeding
Methionine 2	++
Cysteine 2	++
Histidine 2	++
Sucrose 3,4,5	++
Galactose 6	++
Glucose 6	++
Arabinose 6	0
Xylose 6	0
Galacturonic acid 6	0
Polygalacturonic acid 6	--
Methoxypectin 6	0
Arabinogalactan 6	0
Xylan 6	0
Galactan 6	0
Cellulose 6	0
Starch 6	0
Amylose 6	--
Laminarin 6	--
Dextran 6	0
Sinigrin 1,7	++
Amygdalin 7	--
Betulin 7	--
Capsaicin 7	--
Cyanidin HCl 7	--
Diosgenin 7	--
Gossypol 7	--
Hypericin 7	--
Naringin 7	--
Salicin 7	--
Saponin 7	--
Solanine 7	--
Tomatine 7	0
Berberine 7	--
Esculin 7	--
Morin 7	--
Azadirachtin 7	--
Caffeine 7	--
Conessine 7	--
Hordenin 7	--
Phlorizin 7	--
Quinine 7	--
Tannic acid 7	--
Phlorizin 8	--
Phloretin 8	--

1 Nault and Stryer, 1972.
2 Mittler, 1970.
3 Mittler and Dadd, 1964.
4 Mittler and Dadd, 1965.
5 Mittler, 1967.
6 Campbell et al., 1986.
7 Schoonhoven and Derkesen-Koppers, 1976.
8 Montgomery and Arn, 1974.

almost total dependance on conventional pesticides has resulted in a loss of appreciation for and understanding of fundamental biological principles and their incorporation into our applied programs". As the need for new control methods and the concern for the environment increase, the recognition of the importance of basic biological data has to be restored (28) and effort in that field intensified (84). The use of allelochemicals, can be incorporated into plant breeding programs, but an evaluation of the mechanism (95), of the stability of the resistance as influenced by the host-plant and the target insect(s) (28), as well as the individual variability of the pest(s) (55) needs to be understood.

The use of anti-feedant can be incorporated into breeding programs in selecting for a non-preference type of resistance. *S. berthaultii* is presently used in such a way but reports show that the resistance provided by this species can be overcome by the Colorado potato beetle (105). The potato plant's biochemical and morphological characteristics also have to be better known (92). With the generalization of the usage of an anti-feedant, one can expect that the target insect will habituate to the compound, decreasing its effectiveness (7; 20; 84). Examples of this phenomena have been reported for *Schistocerca gregaria*, a polyphagous insect. Due to the difference in host selection mechanism, it is thought to be less likely to occur with oligophagous insects as demonstrated by the field studies with fungicides as feeding deterrents for the Colorado potato beetle (92). Plant resistance can also be useful in retarding the growth of insects as demonstrated with *S. berthaultii* hybrids (21). Slower growth of the insect pest provide more time for biological agents to reach their full potential.

Anti-feedants alone can probably not provide a permanent and perhaps not a satisfactory method of controlling the Colorado potato beetle on potatoes. These compounds can be useful in an IPM program to decrease the population level to an acceptable level. Alternative methods based on feeding inhibition such as repelling adults, inhibition of oviposition by chemicals or modification of plant epidermis, or induction of the production of secondary compounds should be considered . An increase in secondary plant compounds may also increase the level of detoxification of the insect and lower its susceptibility to insecticides (14; 92).

The methodology for the use of semiochemicals is available (9; 89). As summarized by Jermy (46), more has to be known before using semiochemicals in crop protection;

> " Research on the practical use of anti-feedants of plant origin should consider a) the wide capacity of the chemosensory mechanism governing feeding behavior in phytophagous insects, b) the complexity of the 'inhibitory biochemical profile' of plants deterring a given insect species, c) the differences of these profiles in relation to different insect species, d) the variations in feeding behavior of different populations of the same insect species, e) the changes of plant constituents in time and space and f) the problems of formulation of anti-feedants for plant protection purposes."

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CHEMICAL CONTROL AND RESISTANCE DEVELOPMENT IN POTATO PESTS

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ABSTRACT

Numerous pests attack potato and chemical control is used extensively on this crop. With the continuous use of chemicals, several pests, especially the Colorado potato beetle, have developed resistance. The evolution of resistance of the Colorado potato beetle in Canada is describe, with emphasis on the situation prevailing in the Province of Quebec. Factors responsible for this resistance development are discussed and strategies to slow down its appearance are presented. Integrated pest management represents the best technique to cope with the situation.

RESUME

La pomme de terre est l'hôte d'une foule de ravageurs et les pesticides y sont abondamment utilisés. Plusieurs de ces ravageurs, notamment le doryphore de la pome de terre, ont développé une résistance aux insectides. L'évolution de l'apparition de la résistance du doryphore de la pomme de terre est présentée avec un éclairage particulier sur la situation prévalant dans la Province de Québec. Les principaux facteurs responsables de ce développement de résistance sont discutés et des stratégies de lutte alternative sont proposées. Il ressort que la lutte intégrée offre des avantages pour contrecarrer la situation devenue critique dans certaines régions.

INTRODUCTION

Potato production in Canada covers more than 110,000 ha and represents a value of more than 275 million dollars. Unfortunately for the growers, different species of insects attack the potato plant and thus are labeled pests (if not enemies). Table 1 presents the major pests susceptible to attack potato plants.

All parts of the plant are attacked. Wireworms and flea beetles will concentrate on tubers while the Colorado potato beetle, aphids, the tarnished plant bug, and leafhoppers will attack the foliage.

So far, chemical control is the simplest and fastest techique used by growers to control these pests and protect potato plants. But with the continuous use of chemicals, insects developed tolerance or resistance to the insecticides.

Table 1. Major insect pests of potato

Colorado potato beetle	*Leptinotarsa decemlineata* (Say)
Tuber flea beetle	*Epitrix tuberis* Gent.
Potato flea beetle	*Epitrix cucumeris* (Harr.)
Buckthorn aphid	*Aphis nasturtii* Kltb.
Potato aphid	*Macrosiphum euphorbiae* (Thos.)
Green peach aphid	*Myzus persicae* (Sulz.)
Potato leafhopper	*Empoasoa fabae* (Harr.)
Tarnished plant bug	*Lygus lineolaris* (P. de B.)
Wheat wireworm	*Agriotes mancus* (Say)
Dusky wireworm	*Agriotes obscurus* (L.)
Western wireworm	*Agriotes sparsus* Lec.
Prairie grain wireworm	*Ctenicera aeripennis destructor* (Brown)
Gladiolus wireworm	*Ctenicera lobata lobata* (Esch.)
Eastern field wireworm	*Limonius agonus* (Say)
Pacific coast wireworm	*Limonius canus* Lec.
Western field wireworm	*Limonius infuscatus* Mots.

Since the Colorado potato beetle has demonstrated a higher tolerance or resistance development, I will concentrate mostly on this species.

The Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say), is a major defoliator of potatoes throughout much of its range. Historically, insecticidal control has been the major tactic used against this insect (14). The severity of Colorado potato beetle impact on potatoes has resulted in virtually all growers using granular systemic insecticides at planting an additional sprays before harvest.

Insecticide resistance has been a continuing problem in Colorado potato beetle management. A major factor in resistance development is the overuse of insecticides for Colorado potato beetle control. Additionally, pesticides used in potato production (aldicarb and carbofuran in particular) have contaminated groundwater and should no longer be registered for use on potato, especially in sandy soils.

EVOLUTION OF CPB RESISTANCE IN CANADA

In the report of a Work Planning Meeting on insect resistance to insecticides held in Ottawa in 1963 (1), it is stated that: "Resistance to DDT and Dieldrin is reported in the United States but not confirmed so far in Canada". In a survey conducted for that meeting, it was noted that resistance to DDT was suspected on the basis of field observations in Manitoba and on grower reports in southern Alberta.

In Alberta, Colorado potato beetle has been effectively controlled by properly timed and applied sprays. DDT was effective until 1962 at which time DDT resistance became evident in populations from southern Alberta and controls were changed to endosulfan, azinphos-methyl or carbaryl (22). Colorado potato beetle was reported resistant to DDT, aldrin, dieldrin, toxaphene and chlordane by S. McDonald in southwestern Alberta and confirmed by laboratory-controlled tests (11,23).

In Ontario, no evidence of resistance to DDT, endosulfan or other insecticides recommended for control was found by Founk and McClanahan (13), but their tests were restricted to larvae of a single strain and a known susceptible strain was not available for purpose of comparison.

In 1975, McClanahan reported that, since 1971, populations of Colorado potato beetle had been much higher than usual and extensive damage had been caused to freshly planted tomatoes as well as potatoes (21). In 1976, Harris and Svec found strains of Colorado potato beetle resistant to DDT, aldrin, endrin and endosulfan in southwestern Ontario (17).

The first confirmed report of Colorado potato beetle resistance to pyrethroids in Ontario was made by Turnbull an Harris in 1985 (32). A Thedford strain showed a low level of resistance to the pyrethroids tested - cypermethrin, deltamethrin, fenvalerate and permethrin - but was still susceptible to the carbamates, carbofuran and aldicarb.

Studies in New Brunswick between 1982 and 1985 (4) established that 37-fold levels of resistance to carbofuran and phosmet respectively and low level resistance to permethrin, fenvalerate, disulfoton and aldicarb. Resistance, so far, has not spread further (Boiteau, personal communication).

In Quebec, reports were received in 1979 that growers did not get good control of the Colorado potato beetle on several farms near Sherbrooke, Quebec. The main insecticide involved was carbofuran. These growers had used carbofuran, applied as a soil or foliar application, for at least 5 years with satisfactory results before 1979. Other OC, OP, and carbamate insecticides applied as foliar applications in 1979 were not effective against Colorado potato beetle present on these farms. Harris and Svec (18) reported that laboratory tests showed these beetles to be resistant to most of the insecticides currently recommended for use. The level of resistance to carbofuran was very high (> x1, 600). This strain was resistant also to DDT, endrin, endosulfan, azinphos-methyl, phosmet, methidathion, methamidophos, phorate, chloethocarb, and carbaryl. Aldicarb and some pyrethroid insecticides were still toxic to Colorado potato beetle but the results were indicating a slight tolerance to these insecticides and that resistance may also occur in the future.

In 1984, Turnbull and Harris reported the development of resistance to pyrethroid insecticides by the same strain (31). Their results indicated that the Quebec strain showed >20-fold resistance levels to 4 pyrethroid insecticides, cypermethrin, deltamethrin, fenvalerate and permethrin, and that recommended application rate would not be effective against this strain. This phenomenon could be another case where resistance to pyrethroids can often evolve rapidly on the foundation of DDT resistance (15). Since DDT resistance was spread all over the Province of Quebec, reports of pyrethroid failure can be expected in the near future.

The spread of resistance of Colorado potato beetle to insecticides in Quebec followed the most frequently observed pattern: appearance of isolated cases reflecting the distribution and degree of selection pressure. The first observation in Quebec was made in Compton in 1979. Since then, we have determined numerous cases of resistance to O-C's, O-P's and carbamates all over the Province.

Every year, we have more cases reported. Intensive chemical treatment of potato crops have resulted in the selection of a strain whose repertoire of resistance mechanisms has increased rapidly to include almost every insecticide that has been applied for its control, as in the Compton area. In areas where selection pressure has been less severe, resistance does not show up as rapidly (Lac St-Jean and Lower St-Lawrence).

FACTORS INVOLVED IN RESISTANCE DEVELOPMENT

The Colorado potato beetle has the ability to accumulate several mechanisms of resistance. It has been speculated that herbivorus species, which have frequently evolved the capacity to deal with plant alkaloids, are in some sense preadapted to dealing with the problems posed by dangerous chemicals in their environment (7). This presence of several resistance mechanisms, referred to as multi-resistance, made possible the development of Colorado potato beetle resistance to O-C, O-P, carbamate and pyrethroid compounds in Quebec.

Pest selection by insecticides may facilitate evolution of resistance to new insecticides because of cross-resistance. The Colorado potato beetle provides a pertinent example. In Quebec, the populations required several years to develop resistance to DDT, but afterwards, these populations required less time to develop resistance to subsequently used chemicals.

Even though the beetle has only 1 or 2 generations a year, which should delay the appearance of resistance, the high reproductive potential of this species counteracts this fact. As we have seen, the first case of resistance in Quebec appeared in the isolated potato growing area of Compton. Only a few resistant individuals survived treatments with carbofuran. However, because of the smaller number of immigrants in isolated Compton, substantial numbers of resistant individuals were produced.

Many factors can influence the rate of development of resistance. Georghiou and Taylor (16) identified 3 categories of factors influencing the selection of resistance to insecticides in field populations. These are:

A- Genetic factors
B- Biological/ecological factors
C- Operational factors

Most factors in the first two categories cannot be controlled. The factors under man's control lie mostly in the operational factors, such as those related to the timing and dose of insecticide application. The problem is to identify them and determine how their manipulation under the genetic and biological/ecological constraints may retard the evolution of resistance.

Cases of reduced insecticide effectiveness are frequently reported every year. If we go through the Pesticide Research Report, we can see cases reported ever since 1965 on different pests (Table 2). Not all reported cases turned out to be resistance to the insecticide. We have to be careful and investigate each case thoroughly because other factors apart from resistance can bring inadequate control. An incorrect dosage of pesticide will not give adequate control of the pest. Growers have a tendency to reduce the amount of water per hectare to do a faster job. They will also reduce the pressure of the sprayer. A poor spray coverage of the plant gives the pest a better chance to avoid the chemicals. Weather conditions at the time of spraying are also important, especially with the pyrethroids. I have seen growers applying a pyrethroid treatment at 2 o'clock in the afternoon, in bright sunshine when the air temperature was over 25°C. And they were complaining that they were not getting a good control. In rainy springs, the granular insecticide, especially carbamates which are more soluble, wil have a tendency to be washed down into the soil and thus will have a reduced efficacy.

Table 2. Cases of reduced insecticide effectiveness against potato pests.

Pest	Compound	Location	Source
Flea beetles	Aldrin	B.C.	2
	DDT	Quebec	27
	Carbofuran	B.C.	12
		Ontario	22
Aphids	DDT	P.E.I.	6
	DDT	Quebec	27
	Carbofuran	Quebec	29
Wireworms	DDT	B.C.	35, 33
	Carbofuran	B.C.	34
Tarnished plant bug	DDT	Quebec	28
Colorado potato beetle	DDT	Alberta	23
	O-C	Alberta	24
	O-C	Ontario	17
	O-C, O-P and Carbofuran	Ontario	22
		New Brunswick	4
		Quebec (Compton)	18
	Pyrethroids	Quebec (Compton)	31
	Pyrethroids	Ontario	32
	Endosulfan	Saskatchewan	9
		New Brunswick	25,4

Another important factor that can bring inadequate control is bad timing of applications. How many times have we seen farmers starting to spray their potato fields as soon as they see a few CPB on the plants? The treatment will be effective on the insects that are present but not on the ones that will arive afterwards.

Resistance is real and the grower facing this problem will have a tendency to make insurance sprayings by increasing the dosage and the frequency of application. He will also change the pesticide for another one which is usually more expensive. These techniques will bring a many fold increase in direct costs of pest control.

MANAGEMENT OF RESISTANCE

We have to offer the growers some ways of managing resistance. A necessary first step is the development and use of rapid, reliable methods to detect low levels of resistance in pest populations. Immunology, biochemistry, and molecular genetics are expected to play a major role in developing these methods. Also needed are methods to monitor the spread and severity of a resistance episode over time and space in order to gain an accurate picture of the size and speed of resistance development. Table 3 presents results of a test carried out in 1980 on CPB populations of different potato growing areas of Quebec.

Table 3. Susceptibility to carbofuran of CPB adults from different areas of Quebec in 1980.

Area		48 h. avg. corrected % mortality at % insecticide solution		
		.01	.1	1
Quebec	A	58	100	100
	B	28	92	100
Lac St-Jean		16	100	100
Rivière-du-Loup		12	100	100
Nicolet		10	95	100
Joliette	A	10	90	100
	B	0	100	100
St-Rémi	A	5	100	100
London		5	95	100
Ste-Clotilde		0	55	100
St-Rémi	B	0	28	100
Compton		0	0	0

We can see that the carbofuran resistance that had developed in the Compton area was still confined to that area. But in the Ste-Clotilde and St-Remi B areas, the effectiveness of carbofuran was reduced and we could expect problems in the near future. It is also important to monitor the evolution of the effectiveness of chemicals over time. As we can see in Table 4, the toxicity of the chemicals tested against a Ste-Clotilde population decreased from 1981 to 1984, except for aldicarb. These facts are important in the development of a pest management program.

Table 4. Toxicity of several insecticides against adult CPB from 81 to 84 at Ste-Clotilde, Que.

Insecticide	Year	48 h. avg. corrected % mortality at % insecticide solution .01	.1	1
Permethrin	81	5	80	100
	84	5	15	100
Azinphos-méthyl	81	0	5	95
	84	0	0	63
Phosmet	81	0	15	90
	84	0	5	25
Aldicarb	81	0	5	100
	84	0	16	89
Carbaryl	81	0	10	35
	84	0	0	15
Carbofuran	81	3	80	90
	84	0	21	26

A second step would be to recommend strategies to slow down resistance development. These strategies include among others: reduction of frequencies of application, use of less persistent insecticides, treatments based on economic thresholds, and rotation of pesticides. In order to be able to recommend rotation of pesticide, we will have to keep testing the efficacy of new and old chemicals against CPB. The evaluation of insecticides should include not only the LD_{50} and field observations, but also a careful look at the secondary effects of the chemicals. These secondary effects can be negative and/or positive. It has been demonstrated in the past that many insecticides applied against CPB can result in a build-up of aphid populations (Table 5).

Table 5. Insecticides effective against the potato beetle that can result in a build-up of aphid populations

Azinphos-méthyl	13, 8
Carbaryl	13
Carbofuran	8
Phosmet	26, 8
Pyrethroids	19, 30

Recently, Lowery and Sears (20) reported that azinphos-methyl stimulated the reproduction of the green peach aphid. On the other hand, Boiteau *et al*. (3) report that *Myzus persicae* (Sulze) and *Macrosiphum euphorbiae* (Thomas) exposed to aldicarb-treated potato plants are not expected to be efficient vectors of persistent viruses because of a significantly reduced ability to fly and to probe.

Properly considered, resistance management is a component of IPM (10). Since using effective non-chemical control tactics contributes to resistance management, we should help to develop programs for promoting the development and adoption of alternative pest-control methods (biological control, crop rotation, intercropping, breeding for host plant resistance) (5).

Finally, the problem is evident and the need for action is urgent. We must develop pluri-disciplinary programs in order to cope with every aspect of the problem and find answers that will last longer than the pesticides alone. The time has come to sit together and build intelligent programs of pest management.

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INSECTICIDES: SPRAY APPLICATION

by:

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ABSTRACT

The theoretical effects of droplet size and ambient air movements are discussed with regard to the deposition of insecticide sprays on plant targets. Recent developments in spray application technology are reviewed. The results of an experimental study in which spray applications made using an Automatic Mist Concentrate Blower were compared with those made using a conventional boom and nozzle system are presented and discussed.

RÉSUMÉ

Les effets théoriques de la dimension des gouttelettes insecticides et du mouvement de l'air ambient sont discutés en rapport avec la déposition de l'aérosol insecticide sur les plantes cibles. Les développements récents dans le domaine de l'application des aérosols sont passés en revue. Les résultats d'une étude expérimentale comparant les applications par Automatic Mist Concentrate Blower avec celles par le système hydraulique conventionnel sont présentés et discutés.

THEORY

The two most important considerations for a successful pesticide application are (i) to obtain a good deposit on the intended target and (ii) to apply the pesticides at a vulnerable stage of the pest cycle before serious economic damage is done. When considering insect pests on potatoes, the intended target is often both the upper and lower surfaces of the foliage throughout the entire depth of the canopy. In order to formulate an efficient spray technique to achieve this deposit, it is essential to understand the effects of droplet size from the aspect of target coverage and droplet impaction.

Spray droplets can be regarded as spheres and, hence, their volume is defined by the equation:

$$V = 4/3 \Pi \; r^3$$

Where V = volume and r is the radius

Since the volume of the droplet varies with the cube of the radius, this means, for example, that one thousand 50 um droplets will contain as much material as one 500 um droplet. The probability of an insect encountering a spray droplet is directly related to the number of droplets deposited in its microhabitat; therefore, the advantage of small droplets is obvious. Furthermore, large droplets generally contain much more insecticide than is necessary to kill the insect and thereby waste a considerable amount of active ingredient. However, despite the advantages of small droplets, there are potential disadvantages, eg. increased propensity for off-target drift.

As a spray droplet is released it is imparted a velocity by the nozzle. That initial velocity is quickly lost through air resistance. If the drop does not immediately impact upon a surface, its movement becomes subject to two influences - gravity and ambient air movement.

If the drop is large and heavy, gravitational influence dominates over the influence of air movement, with the result that the drop falls or sediments quickly. Due to air resistance, different size droplets have different terminal or sedimentation velocities (Table 1).

Table 1. The effect of droplet diameter on sedimentation velocity in still air

Droplet Diameter	Sedimentation Velocity
250 um	100 cm/s
100 um	24 cm/s
50 um	7 cm/s
25 um	2 cm/s

If, for the present, one ignores evaporation which would gradually diminish the droplet size and, hence, its sedimentation velocity, it is clear that small drops "fall" very slowly. Instead, the motion of small drops will be dominated by air currents and they will track with the ambient air flow - in other words, drift.

Drift, however, is a relative term denoting simply a horizontal component in the droplet trajectory. Efficacy and environmental constraints on the spray application will determine what degree of drift is tolerable, or even desirable, and thereby define the droplet size required for that application.

The predominantly vertical trajectory of large droplets, while an advantage in reducing drift, is often a serious drawback in other respects (1,2). First, if the falling drop encounters a leaf, it will impact on the top surface only. Secondly, if its path does not meet a leaf, it will impact on the soil where it is definitely not wanted.

Large drops, therefore, give non-uniform coverage tending to the upper plant parts and surfaces. Large drops also increase losses to and contamination of the soil. Attempts to counteract the coverage problem have led to the use of very high spray volumes, thereby exacerbating the soil contamination problem through run-off.

Having identified some disadvantages to the movements of both very small and very large spray droplets (without rigidly defining these categories), what then is the effect of drops lying between these size extremes? Obviously, the sedimentation velocities will be intermediate and the drops will be affected both by air movement and by gravity. The trajectories will have both significant vertical and horizontal components, thereby decreasing the probability of impacting on the soil and increasing the probability of uniform deposit on the crop.

Uniformity of coverage by "medium" size drops is aided by air turbulence in the crop canopy. The roughness of the canopy exerts an aerodynamic "drag" on the mean air flow or wind. The "drag" results in a layer of turbulent air extending from inside the canopy to some distance above it. Such mechanical turbulence helps to distribute small drops throughout the crop canopy, with the upward components of the eddies leading to deposit even on the undersides of leaves whereas sedimentation results in deposit only on top surfaces. Turbulence to improve coverage by, and deposition of, small drops can be provided by wind, aircraft wake or fan. Air blast or mist blower sprayers which have long been used in orchard spraying, are finding increasing use in field crops. The basic advantages which they offer, i.e. appropriate droplet size and turbulent impaction as well as lower application rates, reduced water requirements and hence, reduced soil damage due to compaction, appear to have great potential in this industry.

LITERATURE REVIEW

In recent years, spray efficacy studies have shown that by using appropriate droplet sizes, good penetration and coverage of even a dense crop can be achieved with very low chemical application rates, particularly in the presence of adequate air turbulence (3,4,5). The technique has come to be called Controlled Droplet Application or CDA.

While the basic principles of CDA are now very clear, it is essential that the spray parameters be optimised for each type of application. Lacking such experimental optimization, control may still be inadequate (6,7) or only comparable to hydraulic applications (8). Two significant problems must be resolved. First, it is essential to determine the optimum droplet size range and application parameters for a given set of crop conditions (crop structure and pest vulnerability) (9,10,11). Secondly, an atomization device must be found which delivers as much as possible of the pesticide within that desired size range. Finally, the results of such sophisticated research and engineering design must be made available to the grower in a form which is compatible with the realities of his operation.

Innovative spray practices which rely upon judicious choice of droplet size for providing improved and selective crop coverage would be further enhanced if a specific attractive force could be induced between the droplets and the crop surface. To this end, there has been a good deal of time and resources spent in the development of electrostatic spraying methods and equipment. The theory of such a technique is that droplets which can be electrically charged during or after atomization are attracted by electrostatic forces to the crop surface. There are now several experimental and some operational spinning disc, pressure and pneumatic atomizers adapted by addition of auxillary electrodes to produce charged sprays.

The Electrodyne sprayer developed by ICI (12) is a hand held sprayer which relies on an electrostatic field for both atomizing and charging the droplets. Although the sprayer produces a near perfect monodisperse spray with a nmd:vmd ratio of 1:1 (compared to 1:1.8 for a spinning disc atomizer (13) and 1:5 or greater for hydraulic sprayers), only non-aqueous formulations and low flow rates can be used. Spray deposition is quoted as being in the range of 90-100% (14,15); however, the equipment produces a non-divergent spray plume which means that each row has to be treated individually. Furthermore, should the unit come into contact with the crop, not only is droplet charging disrupted, but also the atomization process.

Hybrid systems which only use electrostatics to charge the droplets are not as restricted by liquid properties and can be used to spray aqueous formulations. Charged rotary atomizers have been used in field trials to apply pesticides to both cereals and broad leaved crops (16,17). While improved gross deposition and somewhat improved spray distribution is achieved with the electrostatic effect, there is still a great potential for improvement of spray distribution on the lower canopy leaves and lower leaf surfaces. As with the Electrodyne, it is thought that use of an air blast or other turbulence effect is necessary to achieve this.

With other atomizers such as the Law airblast atomizer (18) and charged hydraulic nozzles (19), the droplets are directed by the nozzle air flow or liquid pressure from the nozzle to the crop surface where the electrostatic charges take effect. In laboratory and field studies on a range of broad leaved crops including potatoes, total deposits were two to seven times greater than equivalent sprays with no electrostatic charges. Spray drift was also reduced (20,21).

Here in Canada, an interesting bi-foil type atomizer has been developed by Inculet *et al*. (22). The equipment consists of two aerofoil shaped linear nozzles, one of which is fed with water and the other with pesticide. A high velocity airstream atomizes the liquid and carries the droplets past two induction charging electrodes. If water is supplied to the uppermost nozzle the emerging droplet cloud essentially consists of an upper cloud of charged water droplets and a lower cloud of pesticide droplets. Since the charged droplets repel each other, the pesticide half of the spray cloud is, in effect, capped and directed down towards the earthed target. Such a method further reduces the potential for drift by the fact that the portion of the spray cloud most likely to drift (i.e. the upper part) consists mainly of water droplets which present no environmental hazards (obviously in a field situation the effects of evaporation must be considered).

In recent years, there has been a welcome trend away from the more traditional experiments in which application methods, dosages and application rates were assessed in terms of the number of surviving insects or eventual crop yield. At last, the scientific community is beginning to realize that interactions of spray spectrum, target deposit and pest populations produce more meaningful results. Future research into field spraying techniques which achieve a good distribution of pesticide in the pest microhabitat must be aimed at optimizing droplet size, turbulence and electrostatic effects. Although experience may show that turbulence and droplet size alone may produce the desired deposit, the work done to date on dense broad leaved canopies has shown that unless electrostatic sprays can somehow be released beneath the canopy or in the presence of turbulence, deposits in the pest microhabitat will be only marginally better than those achieved with conventional equipment.

Although newly developed or novel atomizers might have better atomization characteristics, most farmers already possess conventional boom and nozzle systems to which any new system will be compared (23). The development of retro-fit systems which could be fitted to hydraulic sprayers at relatively low cost to the grower could help to bridge the gap. Such a system is currently being developed in the UK by Lumark Ltd. in cooperation with the National Institute of Agricultural Engineering (Lury, personal communication). As old equipment becomes unfit for use, it can be replaced by more highly advanced systems.

EXPERIMENTAL

In 1985, the Research and Productivity Council (24) carried out an experiment on behalf of Agriculture Canada to investigate the effects of:

(1) insecticide spray applications made under two widely different levels of air turbulence provided by using a hydraulic boom and nozzle sprayer and an Automatic Mist Concentrate Blower*;

and (2) emitted droplet spectrum;

and (3) canopy development ("open" and "closed") upon:

- (a) spray deposition and distribution within the canopy and on the ground;
- (b) reduction of Colorado potato beetle and aphid infestation levels;
- (c) off-target drift.

The experiment was not designed to provide data from which a mass balance could be calculated but to define the relationships between droplet size, turbulence, crop development, spray deposit distribution and insect mortality.

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* Automatic Equipment Manufacturing, P.O. Box P, Pender, Nebraska 68047

The boom and nozzle applications were made on the basis of two-way Anova design with two replicates per treatment. The variables were canopy development - open or closed, and droplet spectrum - "large droplet" spectrum (vmd 175 um, @ 690 kPa) or "small droplet" spectrum (vmd 125 um @ 2070 kPa).

Mist blower applications (vmd ca. 65 um) were designed around a one-way Anova with two replicates per treatment, the only variable being canopy development - open or closed.

A spray mix of Ambush 500 EC**, water and the fluorescent dye, Rhodamine B Extra, was used. Dosage rates were 86-89 g ai/ha and application rates were 500 l/ha and 19 l/ha for the boom and nozzle and mist blower applications respectively. Spray deposit samples were collected from 40 sampling sites covering an area of 18 m X 4 m directly beneath the boom of the hydraulic sprayer and from 130 sampling sites covering an area of 18 m X 35 m downwind of the mist blower. At each site, foliage samples were taken from the upper, mid and lower canopy levels of the potato canopy and ground deposit samplers were placed both within and between rows. In order to qualitatively assess the spray deposit in the mist blower sprays, kromecote cards were placed at all three levels at eighteen of the sampling sites up to a distance of 25 m downwind of the sprayer. Off target drift was assessed using rotorods which were placed at distances up to 100 m downwind of the sprayed area at heights of 1 m, 2 m and 3 m. Spray deposits on both natural and artificial surfaces were quantitated by washing to remove the dye which was then analysed by spectrofluorimetry. Aphid and Colorado potato beetle infestation levels were assessed pre and post spray.

Boom and nozzle applications tended to produce the highest total deposits on foliage with the 690 kPa application deposits greater than those of the 2070 kPa applications. In only one mist blower spray application was a good, i.e. 25 m swath width obtained with total foliage deposit levels comparable to those obtained in the boom and nozzle applications. However, poor spray deposition in the other three mist blower sprays may have been due to either hydraulic problems resulting in volute slip and consequent directing of the spray cloud into rather than across the top of the crop, or application made in highly unstable atmospheric conditions resulting in lofting and drift of the small droplets. In both types of application, total spray deposition decreased with increasing canopy penetration. This effect was more noticeable in closed canopy stands.

The boom and nozzle application resulted in greater proportional deposits on the upper surfaces of leaves, whereas the mist blower's highly turbulent application resulted in much greater proportional deposition on the underside of leaves. The effect was not apparent in Kromecote cards which, except in the very near field, showed most, if not all of the deposit on the upper card surface.

** Ambush 500 EC - Imperial Chemical Industries Ltd.

Spray deposition on the ground varied in inverse proportion to the ground cover provided by the canopy but was much lower in the mist blower applications. Off target drift as measured by the rotorods was minimal for all spray applications.

Despite few data points for the boom and nozzle applications, it would appear from dose response curves that the mist blower produced more effective deposits which resulted in greater aphid and Colorado potato beetle mortality at reduced dosage levels. In view of the greater proportional deposition on the underside of leaves and reduced ground deposit, it is clear that the mist blower has the potential for improving efficacy while minimizing environmental impact at reduced application rates and certainly warrants closer examination.

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SIGNIFICANCE OF PARASITOIDS IN CONTROL OF INSECT PESTS OF POTATOES

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ABSTRACT

Literature pertinent to the significance of parasitoids in control of potato pests in Canada and northern United States is reviewed. The most promising parasitoids are those of the Colorado potato beetle. Two species, the native tachinid fly, *Doryphorophaga doryphorae* (Riley), and the exotic egg parasite, *Edovum puttleri* Grissell, have shown promise but neither is likely to be incorporated into pest control practices at this time due to their slow response to increased numbers of potato beetles. For other pests of potatoes, little or no mortality from parasitoids has been documented in the field. Without considerable research effort in methods of augmentation or mass rearing and release of parasitoids, their role in control of pests of potatoes will remain limited.

RESUME

Ce chapitre analyse la littérature relative à l'importance des parasites impliqués dans le contrôle des insectes nuisibles de la pomme de terre. Le nord des Etats-Unis et le Canada sont couverts. Les parasitoides démontrant le plus de potentiel sont ceux du Doryphore de la pomme de terre. Deux espèces, la mouche tachinide *Doryphophaga doryphora* (Riley), espèce indigène, et le parasite des oeufs, *Evodum puttleri* Grissell, espèce importée, démontrent un certain intérêt. Cependant, leur utilisation dans le cadre d'un programme de contrôle intégré est peu probable dû à leur réponse lente à une augmentation du nombre de Doryphores. Concernant les autres insectes nuisibles de la pomme de terre, les mortalités observées sur le terrain ont jusqu'à maintenant été négligeables. Sans un effort de recherche intensif du côté des méthodes d'élevage en masse et de relargage, leur implication dans tout programme de contrôle demeurera limité.

INTRODUCTION

Information regarding the significance of parasitoids in the control of insects of potatoes was obtained from the literature and from personal communications with researchers in Canada. The pests considered were those commonly found on potatoes in Canada and northern United States. They included the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), the green peach aphid, *Myzus persicae* (Sulzer), the potato aphid, *Macrosiphum euphorbiae* (Thomas), the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), the potato leafhopper, *Empoasca fabae* (Harris), and the potato flea beetle, *Epitrix cucumeris* (Harris). Lists of parasite-host records or observations from early literature were not cited. Emphasis was placed on information that described the effects or potential effects of parasitoid insects on pest populations.

Colorado Potato Beetle (CPB)

There are only two parasitoids of this pest that have been investigated to any degree in North America. The first is Doryphorophaga doryphorae (Riley), a tachinid larval parasite that attacks second- to fourth-instar larvae. The second is the eulophid egg parasite, Edovum puttleri Grissell. Neither parasite has been integrated into a management program, but both have been evaluated for their effect on suppression of populations of CPB.

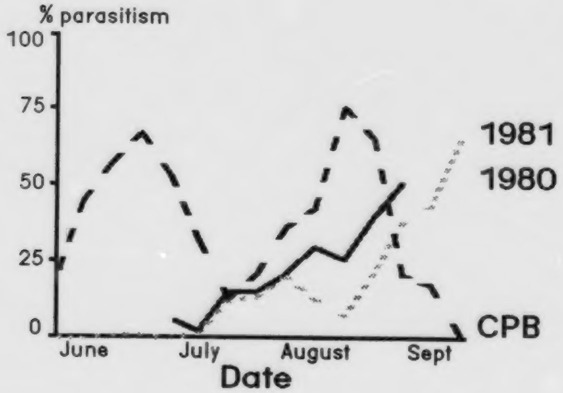

Fig. 1. Parasitization of Colorado potato beetle, Leptinotarsa decemlineata (Say), by the tachinid parasite, Doryphorophaga doryphorae (Riley), in 1980-81. (Redrawn from Tamaki et al. 1983).

Biology of D. doryphorae has been described by Franz (7) and Kelleher (13). However, it was shown that the parasite was not effective in controlling populations of CPB due to its slow response in the early season (14, 9). Kelleher (14) reported that 30 to 60 percent of larvae and pupae were parasitized. The proportion of the population that were parasitized increased during the latter half of the season. Harcourt (9), in a life-table approach, indicated that D. doryphorae accounted for between 0.5 and 27 percent mortality of pupae of CPB over a six-year period in Ontario.

More recently, Tamaki et al. (25, 26, 28) have attempted to evaluate the impact of this parasite on populations of CPB in Washington and to suggest methods for enhancement of mortality by the parasite. They found that mortality by the parasite increased as the host population increased, especially during the second generation (Fig. 1). Parasitism was less than 2 percent in June during the early part of the first generation, increased to 15 percent during the latter part of that generation in mid-July, was 30 percent during the first part of the second generation and reached 70 percent by late August at the end of the second generation.

Limitations on the effectiveness of this parasite include poor survival during the winter or poor synchrony with its host in the early season. Another factor is the lag in emergence of the adult parasites that had been deposited as first-instar planidia in second- or third-instar host larvae. This delays the emergence of parasites from hosts in the early stages of the first generation and may account for the slow increase in rates of parasitism until the latter half of the season.

Rearing methods have been outlined for this parasite (13, 27), but inundative releases have not been documented. The effects of some insecticides on populations of the parasite under laboratory conditions have been described (28). Diflubenzuron, a growth regulating hormone mimic, did not affect development of larvae with host larvae that were reared on foliage treated with solutions of 50 mg/L active ingredient. Above this value, survival of parasite larvae decreased considerably.

The exotic eulophid parasite, E. puttleri, was collected in Colombia, S.A. in 1980 and brought to the United States, where the small colony was screened for potential hosts (20). Eggs of CPB and another species of Chrysomelid beetle, Labidomera clivicollis (Kirby), proved to be the only hosts that were acceptable to this parasite. Eggs of L. undecemlineata (Stal), the South American host, are larger and produce more robust parasites. This host is used in an outdoor mass-rearing program in Texas to supply large numbers of parasites to release locations within the United States (R.W.F. Schroder, USDA, Beltsville, MD., personal communication). This parasite attacks the host egg mass, parasitizes ca. 30 percent of the eggs and feeds upon (causing mortality) an additional 60 percent of the eggs. Overall host mortality of egg masses in laboratory trials approaches 90 to 95 percent (22).

In laboratory experiments, parasites performed well at temperatures between 18 and 29°C (19). They did not survive below 15°C. Development of the immature stages within the host egg took 14.3 days at a constant temperature of 24°C. Development of parasites in the field required from 19 to 28 days, depending on heat units accumulated in each location. Survival of adult parasites caged with egg masses and placed in the field during the fall was nil by the end of November. They concluded that this parasite was poorly adapted to the climate in northeastern United States.

Inundative releases of E. puttleri have been performed in plot trials and in commercial fields in a number of locations in the United States. Few results have been reported in the literature. Cantwell et al. (3) sprayed suspensions of Bacillus thuringiensis var. thuringiensis in conjunction with releases of E. puttleri to control Colorado potato beetles on tomatoes in Maryland. The applications of B.t.t. alone or in combination with E. puttleri reduced the numbers of large larvae of the potato beetle. Releases of E. puttleri alone did not affect the populations of potato beetles. Results from other locations indicated only slight reduction of potato beetle populations following releases of E. puttleri (R.W.F. Schroder, USDA, Beltsville, MD., personal communication).

Rates of parasitism for PA are similar to those recorded for GPA (24, 21). Recent research has concentrated on the parasitoid *Aphidius nigripes* (Ashmead) and its host-finding ability (1, 2) and its ability to discriminate among hosts (4, 5). Females of this species respond to host odors secreted in honeydew of the PA. They also responded to odors of related host aphids (1, 2).

As was reported previously for parasites of GPA, *A. nigripes* was able to distinguish parasitized PA but this ability only lasted for an hour or two (4). As host density increased, parasite activity increased which led to superparasitism (4).

In Quebec, rates of parasitism of PA by *A. nigripes* in fields of potatoes reached 30 percent at the end of the season, but many of these were attacked by hyperparasites (C. Cloutier, Laval University, Quebec, P.W., personal communication). *A. nigripes* was slow to respond to increasing populations of PA and did little to regulate the population. Poor response of *A. nigripes* to increase in populations of PA and low survival over winter limit the effectiveness of this parasitoid.

Tarnished Plant Bug (TPB)

Tarnished plant bugs are occasional pests of potatoes in Canada. Parasitoids have been associated with TPB in Canada and other parts of North America. In Ontario, the braconid parasitoid *Peristenus* (= *Leiophron*) *pallipes* (Curtis) and *P. pseudopallipes* (Loan) attack populations of TPB in forages and weeds (15, 16). No reports of the activity of these parasites in potatoes is available. Two other species have been recently introduced into Saskatchewan -- *P. digoneutis* Loan and *P. stygicus* Loan (6). These releases occurred in alfalfa and again may not be of significance to TPB in potatoes.

In Arizona, a mymarid egg parasitoid, *Anaphes ovijentatus* (Crosby and Leonard), performed well in the laboratory (12). It parasitized *ca.* 60 percent of the TPB eggs provided and may have reduced the viability of additional eggs.

Potato Leafhopper (PLH)

Very little information beyond faunal lists and occasional observations regarding parasites of the PLH is available. Freytag (8) lists the species reared from the PLH. These include the dryinid wasp, *Aphelopus* sp., a parasite of the adult leafhopper, and several species of mymarid egg parasitoids that include, *Anagrus armatus* (Ashmead), *A. nigriventris* Girault and *A. epos* Girault. No information on the rate of parasitism by these species on PLH is available. Their effect on populations of PLH in potatoes is likely minimal.

Potato Flea Beetle (PFB)

No recent information was obtained regarding the effect of parasitoids on populations of the PFB.

E. puttleri was imported to Canada, mass-reared in the Biological Control Laboratory at the University of Guelph, and released in field plots at Fredericton, New Brunswick and at Guelph, Ontario during the seasons of 1982 to 1984. Results varied from year to year and at each location, but the capability of this parasitoid to suppress populations of CPB was established (Sears and Boiteau, unpublished). Mortality of host eggs by parasitism and host feeding exceeded 70 percent at Guelph in 1984 and reached 75 percent at Fredericton in 1985. Lower levels of parasitism were recorded in the other years at each location. These maximum rates of parasitism were recorded late in the first generation (of a single generation of CPB per year in Fredericton) or in the second generation at Guelph (two generations of CPB per year in Ontario).

Even though it was released in large numbers at the time of first oviposition of CPB in the spring, parasitization and host feeding by E. puttleri at that time never exceeded 20% at either location. Subsequently, in laboratory experiments, it was found that activity of this parasitoid decreased significantly at temperatures below 20°C. When daily maximum and minimum temperatures were examined at each location during the periods of field release of E. puttleri, this inactivity of E. puttleri at lower temperatures was corroborated (Sears and Boiteau, unpublished).

Green Peach Aphid (GPA) and Potato Aphid (PA)

Many species of hymenopterous parasitoids, primarily in the families Aphidiidae and Aphelinidae, are associated with aphids that infest potatoes, but few are host specific. Aphid densities on potatoes are generally low which makes control by parasites less effective. On potatoes, aphids are of particular interest as vectors of disease organisms. Emphasis is placed on preventing initial feeding by immigrant individuals and preventing these localized infestations from becoming widespread. Regular applications of insecticides for control of other pests often preclude any benefit from parasites in the control of aphids.

Recent research with parasites of GPA have focused on the response of the parasites to host populations in protected environments (10, 11). Under these conditions the parasite, Ephedrus cerasicola, demonstrated a functional response to increasing densities of GPA. However, as the density of parasites increased, superparasitism increased proportionately. Parasites were not able to discriminate between parasitized and unparasitized hosts after only an hour from a previous encounter.

Over 30 parasites of GPA have been identified (17). In Maine, parasitism of GPA in potato fields averaged 0.14% over an 18-year period from 1952 to 1969 (24, 23). The highest yearly average was only 0.63 percent. There was no correlation within years or over the entire study between rates of parasitism and density of aphids. In more general surveys in different areas of the world, rates of parasitism never exceeded 1.5 percent (18, 21). In all these studies, hyperparasitism was high and ranged from 22 to 53 percent of parasitized GPA.

SUMMARY

Parasitoid insects have not proven to be important in the regulation of insect pest populations on potatoes. The most encouraging results have been in regard to the tachinid parasitoid *D. doryphorae* and the eulophid egg parasitoid, *E. puttleri*. Neither of these beneficial insects is likely to be incorporated into pest control practices in Canada due to poor synchrony with their host, inability to overwinter, or slow response during cool weather. A number of parasitoids have been identified and examined from aphid pests of potatoes. Despite the amount of attention they have received, they are not likely to provide significant control. As for parasitoids of other common pests of potatoes, little information on their effect on host populations in potatoes is available. They are also not likely to provide sufficient population regulation to be of economic importance.

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THE SIGNIFICANCE OF PREDATORS AND CULTURAL METHODS

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ABSTRACT

In most of Canada, aphids and the Colorado potato beetle are the major insect pests on potato. Only very small numbers of aphids can be tolerated on the potato crop because they are vectors of important virus diseases. This limits the contribution of predators to their control. Also, the parthenogenetic reproduction of the aphids ensures a reproduction rate superior to the one of sexually reproducing predators. However, studies have demonstrated that native predators do exert some control of aphid populations. The level of control could be optimized by reducing the impact of other control strategies on predators. Also, cultural methods or cultivars reducing the reproductive capacity of the aphids would be desirable. Native predators of the Colorado potato beetle are almost nonexistent. The introduction of predators from South America needs to be considered but cultural methods such as crop rotation offer the greatest potential for new control strategies.

RÉSUMÉ

Les pucerons et le doryphore de la pomme de terre sont les principaux insectes nuisibles sur pomme de terre pour la plupart des regions du Canada. L'abondance des pucerons doit etre maintenue a de tres bas niveaux parce qu'ils sont des vecteurs de maladies virales importantes. Cette exigence limite la contribution des predateurs a leur controle. De plus, la reproduction parthenogenetique des pucerons leur assure un taux d'accroissement superieur a celui des predateurs qui eux se reproduisent sexuellement. Il n'en demeure pas moins que les predateurs indigenes peuvent exercer un certain controle des populations de pucerons. Le niveau du controle obtenu pourrait etre accru par une reduction de l'impact sur les predateurs des autres techniques de controle. L'utilisation de methodes culturales ou de varietes qui reduisent le potentiel reproducteur des pucerons serait aussi desirable. Le predateurs indigenes du Doryphore de la pomme de terre sont presque inexistant. L'introduction de predateurs depuis l'Amerique du Sud doit etre consideree mais les methodes culturales telles la rotation des cultures offrent le meilleur potentiel pour le controle.

INTRODUCTION

The role of predators in insect protection on potatoes in Canada has been a source of interest for over 60 years (26). Canada and the USA were visited by Europeans in search of natural predators of the Colorado potato beetle (CPB) pest that had recently been introduced on their continent (e.g. 72).

More recently, a 3-year survey of the potato fauna in New Brunswick identified more than 560 species or group-species of arthropods that can be present in potato fields (6 and 7). Of these, 23% can be considered predaceous (32% aphidophagous, 16% prey on small insects and eggs, 52% are general predators). Even though the majority are uncommon or transient species, their diversity suggests a possibly important role in the control of the 22 or so species of pests (29).

Canadian potato growers, like growers elsewhere, have always been good observers of their natural environment. By trial, they learned to adopt cultural practices that reduce the abundance of pests and protect plants. The advent of modern insecticides gave central importance to rapid increases in yield, sometimes at the expense of sound ecological management of crop and pests. As a result, potato production today relies heavily on chemical control and very little on cultural methods to control pests.

I have reviewed most of the Canadian literature available on potato pest control by predators or cultural methods. Because of its sparcity, I also included results of relevant research studies from elsewhere, particularly North Eastern North America so some assessment of the significance of these methods could be conducted.

PREDATORS

Predator fauna:

The fauna of potential insect predators in potato fields in Canada consists mostly, in decreasing order of abundance of: Carabidae, Arachnida, Staphylinidae, Coccinellidae, Syrphidae, and Chrysopidae (6) (Table 1). On the canopy, the Coccinellidae are the most frequently observed predators, even though their numbers are never very large. Elliott (21) reports observing various aphid predators in Ontario potato fields but counted only 10 coccinellid larvae and 1 chrysopid larva in 9210 leaf samples taken between 1969 and 1971.

The Canadian predator fauna is similar to the one of the New England States. In Pennsylvania, of 21 species of arthropod predators found on potato foliage, eight were Coccinellidae (43).

Table 1. Orders and families of arthropods preying on potato insect pests in Canada.

Class	Order	Family
Arachnida	Araneida	
Insecta	Coleoptera	
		Carabidae
		Cantharidae
		Coccinellidae
		Staphylinidae
	Diptera	Syrphidae
		Cecidomyiidae
	Neuroptera	Chrysopidae
		Hemerobiidae
	Heteroptera	Anthocoridae
		Lygaeidae
		Nabidae
		Pentatomidae
		Saldidae

Table 2. Effect of ground beetle exclusion on populations of potato aphids in New Brunswick.

	1981		1982		1984	
	Beetles	Aphids	Beetles	Aphids	Beetles	Aphids
Fence plot	445	389	604	1583	301	886
Check plot	1682	335	1441	1563	933	507
Change (%)	-75	+16	-58	+1	-68	+55

ARACHNIDA

Spiders were among the most abundant general predators found on potatoes in New Brunswick (7). In Pennsylvania, they were the second most abundant group of polyphagous predators (43). There, they were observed to feed on the potato leafhopper but never on the green peach aphid. On the foliage, Misumenops sp. (Thomisidae) and Tetragnatha sp (Tetragnathidae) were the most abundant. Shands et al. (62) believed that spiders because of their distribution throughout the season and their mobility were probably the most important predators of aphids.

The role of spiders in biological control was reviewed by Riechert and Lockley (55). They concluded that the application of spiders to the pest control effort can best be achieved in perennial agricultural systems like orchards where disruption is at a minimum. On a species basis the role of spiders appears limited. The spider community as a whole seems, however, able to buffer pest populations at low densities.

Harvesting, tilling and insecticide applications on agricultural crops are all disruptive of the spider community.

COLEOPTERA

Carabidae:

The Carabidae are one of the most abundant group of polyphagous predators in potato fields (7). The genera *Harpalus*, *Agonum*, *Pterostichus* and *Carabus* represented 95% of all specimens collected in a New Brunswick survey (8). Their abundance varied between years but the generic and species composition did not. The density of Carabidae decreases with the distance from wooded borders (36 and 8), affecting the degree of control throughout the field.

Trouvelot (72) reports *Lebia grandis* as an important predator of CPB in North America. Only a few specimens of *Lebia* sp. were found in the New Brunswick survey, perhaps because they prefer sandy areas.

The reduction of populations of Carabidae in potato plots with enclosures did not change significantly the aphid populations although there was a tendency for larger aphid populations in plots with depleted populations of Carabidae (10) (Table 2). Karg (36), in Poland, calculated on the basis of CPB remains in field transects and laboratory feeding tests that predaceous Carabidae could theoretically eliminate 0.21 adult CPB/m^2 and 1.57 L4/m2 during a season. This is only a very small percentage of a CPB population.

Coccinellidae:

More than 90% of species of Coccinellidae are predatory (22). They are the most abundant predators on potatoes at the canopy level (7) in Canada. Very voracious, Coccinellidae have been found to have significant potential for pest control on many crops throughout the world but their role has been generally unpredictable, variable from year to year.

At least 16 species can be found in Canadian potato fields, the most common being *Coccinella transversoguttata* Brown (7). Its biology, under laboratory conditions, has been studied by Lesaffre (41). Only 2 specimens of *Anatis quindecempunctata* Oliv. were found in 1979-1981 in New Brunswick (7) even though it had previously been reported as an important predator of the CPB (26). Since 1981, the seven spotted ladybeetle, *Coccinella 7-punctata* (L.), a very polyphagous introduced species has been spreading throughout Eastern Canada and has become the most common species in many potato fields (Specht, personal communication; Boiteau, unpublished). *C. septempunctata* is now found in 5 Canadian provinces (Schaefer et al. unpublished). The effect of this introduction on the community of Coccinellidae is poorly documented.

As in Canada, *C. transversoguttata* is the most abundant species in New York followed by *Coleomegilla maculata* DeGeer and *Hippodamia convergens* Guerin-Meneville (53). In Pennsylvania, *C. maculata* is the most abundant adult coccinellid in groundcloth samples and *H. convergens* in sticky trap samples (42). This apparent discrepancy is attributed to the greater mobility of *H. convergens*.

Mathematical simulations showed that C. maculata cannot prevent green peach aphids [Myzus persicae (Sulzer)] from causing serious damage to the potato crop in normal cool, early growing seasons (46) in the New England States. The predator requires a higher temperature, 3rd instar larvae and adults being most effective in reducing the aphid population in temperatures above 29°C (46). This is not unexpected considering that its optimum temperature range for development is 24-26.7°C (66, 52 and 76). The theoretical developmental threshold for C. maculata is between 9 and 13°C (52).

Ladybugs can cause severe damage to egg masses of CPB but their numbers seem to be regulated by the abundance of the aphids, not by the abundance of CPB eggs (73). Their potential for CPB control is therefore limited in Canada where aphid populations are generally at low levels of abundance.

Staphylinidae:

Another of the most abundant group of polyphagous predators in potato fields (7). Essentially nothing is known on their potential for potato pest control.

DIPTERA

Syrphidae:

Most syrphid larvae are predatory and generally polyphagous. Data from New Brunswick indicate that the abundance of Dipteran larvae is relatively low and, perhaps of more importance, varies widely between years (7). Mack and Smilowitz (43) found very few syrphid larvae on potatoes in Pennsylvania during the 1977 season while sampling with groundcloth.

Cecidomyiidae:

Although most species of Cecidomyiidae are phytophagous, the larvae of many species are predatory on aphids. Their role in biological control is thought to be limited because larvae are not very mobile and many are very prey specific (22). A predator on M. persicae in glasshouses, Aphidoletes aphidimyza (Rondani) is commercially produced by a Finnish company (48 and 30).

NEUROPTERA

Most adults and larvae of Chrysopidae and Hemerobiidae prey on aphids. However, densities of larvae and adults of Chrysopa sp. and Hemerobius sp. are very low in potato fields (43, 42 and 7).

In Manitoba, Kelleher (37) attributed some of the high CPB egg mortality he observed between 1957 and 1959 to predation by Chrysopidae. The cold rainy weather may have been an even more important control factor or may have assisted the predator. In Russia, Shuvakhina (63), found that the effect of Chrysopa carnea Steph. was very much affected by the effect of weather conditions on the complex predator-CPB-plant relationship. Releases were most effective early in the season when the CPB was ovipositing at a low rate (64). Over a period of three years, yields were maintained with predator-prey ratios of 1:10 and 1:26 (egg masses). Releases of 2nd and 3rd instar larvae gave better control of populations of CPB than releases of eggs.

HETEROPTERA

Very polyphagous, some of these species can attack beneficial as well as pest insects, putting some questions on their role as control agents (22).

Anthocoridae:

Orius sp. was found in New Brunswick potato fields in 2 years of a 3 year survey and in low numbers (7). In Pennsylvania, *Orius insidiosus* (Say), the minute pirate bug, was the most abundant polyphagous predator on potatoes but was observed to feed only on the potato leafhopper, *Empoasca fabae* (Harris) (43).

Lygaeidae:

In New Brunswick, *Geocoris* sp. was present in low numbers in potato fields in two of a three year study (7). *Geocoris* spp. were the most abundant predators on potatoes in an alfalfa interplant study in Washington State (70). Their actual effect on the aphid population was not reported. Tamaki and Weeks (70) do provide a thorough analysis of the biology and ecology of *Geocoris* spp..

Nabidae:

Nabidae are present in low numbers in New Brunswick potato fields (8). In Pennsylvania they are the least abundant polyphagous predator collected (43).

Pentatomidae:

The two-spotted stink bug, *Perillus bioculatus* (Fabricius):

Studies and attempts to establish this predator have been made in more than 8 countries, including the USA (69). In most countries, it did not become established but required reintroduction. In Ontario, it is naturally very abundant [with *P. circumcinctus* Stal.] in some years according to Gibson et al. (26). However, a report of a 1957 survey indicates low numbers of the predator in Ontario and no significant control (1). Tamaki and Butt (69) present a complete study of the bionomics of *P. bioculatus*. In summary, a population of two-spotted stink bugs can double its size in 8 ½ days at 22°C for a generation time of 47 days. Instars 2-5 consume an average of 0.098-0.238 L3 or L4 per day. The authors calculated that to reduce a CPB population of 31 larvae/plant to zero in 7 days would require 1.15 predator/plant. High populations of *P. bioculatus* in the field in Washington State were estimated to be less than 0.5/plant. *P. bioculatus* never wastes food and even seems to prefer to share a larva with another bug. Each larva is eaten entirely before moving to another one (68). The predator was found able to reduce defoliation by small populations of CPB but not by large densities. Tamaki and Butt (69) showed theoretically that in Washington State, in spite of a good potential against the pest, P. bioculatus does not prevent significant yield losses under field conditions. Earlier, Trouvelot (72) reported that isolated cases of rapid multiplication of P. bioculatus had almost exterminated populations of CPB in North America. Trouvelot also observed that this predator requires a mild winter and an abundance of shelter for hibernation.

The spined soldier bug, Podisus maculiventris (Say):

The spined soldier bug is a polyphagous predator previously identified as an effective control agent of some crop (e.g. alfalfa) and tree pests. In Nova Scotia, it is a predator in apple orchards (47). Because of its potential in orchards, fairly detailed studies of its ingestion process, the effect of predator age on functional response, the effect of prey size, growth and food consumption were completed at Macdonald College and the University of British Columbia (50, 51 and 25).

The spined soldier bug overwinters in Eastern United States and Canada (40). Instars 2 through 5 are predaceous. The 2nd and 3rd instars consume approximately 1.5 small CPB larvae per day and 4th and 5th instars approximately one large CPB larva per day. However, laboratory tests by Drummond et al. (19) indicate that the CPB is a poor host: of 4 preys tested, the CPB provided the lowest developmental and survival rates. In Poland, Pruszynski and Wegorek (54) had previously made similar observations. In addition, Pruszynski and Wegorek (54) found that fecundity was at least two times less on CPB than on the Mediterranean flour moth. These differences can be lessened by allowing P. maculiventris to feed on the host plant at the same time (56). It was also observed, in the laboratory, that the bugs will kill a much larger number of CPB larvae than required for feeding; the greater the number of larvae offered as prey, the greater the number killed. Also, the predator has a developmental threshold of 15°C compared to 10°C for the CPB, giving a developmental advantage to the CPB. By simulation, Drummond et al. (19) showed that, in areas with low spring temperatures (e.g. Rhode Island), the predator would average a 23% longer developmental period than the CPB. These observations explain in great part why the spined soldier bug is usually found in low densities in potato fields. A release of 14,000 larvae and adults of the predator in a 1000 sq m potato plot in Poland is said to have resulted in a greatly reduced population of CPB in spite of an important emigration of P. maculiventris to neighbouring plants and shrubs (54). Polish researchers are more positive than the Americans on the potential of P. maculiventris, considering it an especially good candidate for multiple farming operations, possibly those including orchards.

BIRDS

Birds are considered predators of CPB in many countries of the world. In Canada, the Rose-Breasted Grosbeak feeds on both adults and larvae (it has been called the "potato-bug bird") (26). Other birds feeding on CPB are: bob-white, ruffed grouse, sharp-tailed grouse, cardinal, yellow-billed cuckoo, nighthawk and prairie chicken. They seem, however, to play a very minimal role in control (32). Symptoms of poisoning have been observed in starlings feeding on larvae of CPB (73).

The predator complex:

The concept of a predator complex was applied to potatoes by Tamaki (68). In this approach, all species of predators attacking a pest at a given time become one unit, an idealized predator species. In evaluating this "species", it is important to consider its relationship to the population growth phase of the pest. Natural biological control will be relatively effective when the predator complex contains a number of different species that attack the pest in all three phases of its population growth. This is lacking for the CPB. For aphids, mainly pests as vectors in Canada, the emphasis must be placed on the establishment phase of the pest population because the economic threshold for the pest is extremely low, close to zero. Predators during this phase need not to have high prey consumption rates (68) but must be fairly abundant and have good searching abilities.

Natural enemy sampling procedure:

Boiteau (7) used sweepnet, groundcloth, yellow water trays and pitfall traps to draw an inventory as complete as possible of the arthropod fauna of potato fields in New Brunswick. In Pennsylvania, where the Coccinellidae were identified as the major predators, Mack and Smilowitz (43) concluded that the groundcloth method was better than the sweepnet because it more accurately estimated the size of the larval population of Coccinellidae. They recommended sampling in the morning to minimize variations in the counts caused by diurnal variations in the abundance of C. maculata, C. transversoguttata and H. convergens (42).

Modeling:

Whalon and Smilowitz (75) developed a computer forecasting system for the management of green peach aphid on potatoes in Pennsylvania. Later, a predator-prey model simulating the interactions of C. maculata and M. persicae was included (46). Tamaki (70) developed a predictive model based on the reductive impact of the predator complex on the potato pests. No similar efforts have been made in Canada.

Vertical distribution of preys and predators:

Ideally, the vertical distribution of prey and predator populations on the potato plants should coincide to maximize the encounters. In New Brunswick, GPA are found in ratios of 1:5:8 to 1:1:2 on the top, middle and bottom leaves depending on the variety (14). This is similar to Duncan and Couture (20) in Quebec who found 6, 17 and 77% of GPA on the top, middle and lower portion of the plants respectively during a 5 year study. This is also the area where most of the adults of at least one of the species of Coccinellidae, C maculata, seem to occur (44).

Plots treated with insecticide by Boiteau (10) saw a greater resurgence of Macrosiphum euphorbiae (Thomas) than Aphis nasturtii Kaltenbach. This could have been--at least partly (10)--the result of different predation levels. The distribution of the potato aphid on the upper portions of the plant (14 and 20) exposes it to predators working the canopy. On the other hand, insecticides may alter the vertical distribution of aphids on potato plants (44). This in turn could affect the effectiveness of predators in locating the prey.

Effectiveness of predators:

The consistent presence and the even distribution of ground predators (6) suggest that they could play an important role in the control of potato pests. Experimental tests using enclosures and insecticide treatments showed, however, that the ground fauna, especially the Carabidae, play in fact a minor role in aphid control (10). The tests revealed a much more significant potential for predators at canopy level. Exclusion techniques were used earlier to determine the effectiveness of natural enemies in reducing populations of CPB in Ontario (23). Conclusions were that birds and crawling insect predators did not increase control but flying insects, particularly P. bioculatus, did.

Trouvelot (72) reported that natural enemies reduced populations of L. decemlineata in North America by 10-20%. In New York in a study using individually caged plants, Obrycki et al. (53) found that natural enemies generally resulted in 65% reduction of aphid populations. In Maine, Shands et al. (59) reduced peak aphid numbers by 26-70% by releasing Coccinella septempunctata, Coccinella transversoguttata and Chrysopa spp.. Elimination of natural enemies in potato plots in Pennsylvania resulted in populations of GPA fifteen to a thousand fold greater than in those plots where natural enemies were conserved (65). Shands et al. (62) concluded after many years of field observations that predators were less important than fungi but more important than parasites in controlling aphid populations on potatoes.

In France, Boczkowska (4) reported a significant reduction of CPB populations in her field plots caused by natural enemies.

It may be tempting to use the efficiency data for some predators on another crop and extrapolate it to potatoes. It is often the only information available. This evidence must be used with caution though. Many factors differ between different plant cultures. Tamaki et al. (71) have shown, for example, that predators (Coccinellidae, Geocoris sp., Nabis sp., etc.) were 2-5 X less active on broccoli than on radish or sugarbeet plots infested with M. persicae.

The role of predators in the control of potato pests will be affected by the presence of their own parasites and predators and by the interference and competitive behaviour of the complex of predators (e.g. 57). To give some measure of its importance, I will mention that the parasitism rate of aphid predators on cereals in England was found to reach 25% (18).

Compatibility of glandular pubescence and biological control:

Glandular pubescence is being used in potato breeding as a defense against aphids, leafhoppers, potato flea beetles and Colorado potato beetles. In greenhouse studies, the glandular pubescence was shown to inhibit the movement of first instar Coccinellidae (53). However, in the field, the trichomes did not seem to affect predation in any measurable way (53).

Predation on overwintering hosts:

Predation of the aphids on their overwintering hosts can be important. In Maine, Shands et al. (60) report having to survey aphid colonies as early as possible in the spring or many of the aphid "colonies" would have been cleaned out by predators and parasites. In Maine, Shands and Simpson (58) found the predators to be of no appreciable importance in limiting the fall abundance of the buckthorn aphid on alder-leaved buckthorn. However, in the spring, the larvae of syrphids and Scymnus sp. have occasionally reduced substantially the number of potential spring migrants on buckthorn (58). In the case of the potato aphid, spiders were the most effective predators in the fall on swamp rose (61). In the spring, several species of spiders and coccinellids were very important and, occasionally, some larvae of syrphids and chrysopids.

CULTURAL CONTROL

Planting date and location:

By planting as early as possible, using short season varieties whenever possible, it is possible to topkill the crop before the GPA inflights are too severe in Atlantic Canada (9 and 13). Delaying planting dates would ensure lower numbers of potato and buckthorn aphids but would expose the crop to the full duration of green peach aphid flights. Other cultural methods, such as roguing and planting high quality seed, have had little or no effect on the aphid vectors themselves but have resulted in significant controls of the diseases (e.g., 5).

It seems generally accepted that potato fields should be located on windswept land and without windbreaks to reduce the deposition of the pests that are carried in the air currents. These fields tend to have reduced snow cover. It has often been reported that large numbers of beetles fail to live through the winter if the ground is not protected from frost by snow (e.g. 26).

Management of overwintering sites:

The removal of winter and spring reservoirs of vector populations could supplement natural biological control. This has been somewhat successful in Washington State (67) against the GPA populations in cultivated orchard floors. In Maine, the attempted eradication of Prunus nigra, the overwintering host of the green peach aphid in North Eastern USA and much of Canada, does not appear to have had much of an impact. It could be that the eradication was incomplete, that GPA populations from greenhouses and bedding plants constitute the main source of GPA moving to potato fields or that the GPAs immigrate from other States where they overwinter in orchards. A larger scale control of overwintering sites might be required to affect GPA populations on potatoes.

Greenhouses are another major source of aphids for early infestations. A survey of greenhouses in the potato growing areas of New Brunswick between 1971 and 1975 revealed that most were infested with three of the potato colonizing aphid species. A substantial percentage of the bedding plant outlets inside and outside potato growing areas can also serve as aphid reservoirs (Table 3). Growers should make sure that neighboring glasshouses use adequate controls.

Table 3. Incidence of aphids in beeding plant outlets in New Brunswick, 1975-1977

Year	Establishments	
	Visited (#)	Aphid infested (%)
1975	60	50
1976	73	45*
1977	66	14

*77% M.p.; 10% A.s.; 5% M.e.

Mixed plantings:

It happens occasionally that growers plant a portion of a field to a variety and the rest to another one. Could such fields be more or less resistant to insect pests? There is little information on the subject. Cantelo and Sanford (17) found that, in mixed stands of a susceptible and a resistant cultivar, the potato leafhopper had lower densities than in pure stands of the susceptible cultivar but generally higher densities than in the resistant stand.

Plant density:

The density of potato plants is likely to affect the distribution of predators in the stand. In cereals, Honek (31) has shown that species of the genus *Coccinella*, able to regulate body temperature, prefer sparse stands. By contrast, syrphid larvae whose integument is soft and more susceptible to desiccation prefer the humid microclimate of dense plantstands.

Undersowing:

In Great Britain, McKinlay (49) reduced populations of *M. euphorbiae* and *M. persicae* on potatoes by undersowing with perennial ryegrass. Undersowing did not reduce colonization but probably increased shelter for predator populations. Tuber yields were not affected but there were significantly more small sized tubers in the undersowed than in the potatoes alone.

Interplants and border plants:

Interplants or border plants of a crop that do not serve as a reservoir for aphid vectors or a disease, but serve as a reservoir for predators, might be helpful in providing biological control of an aphid like Macrosiphum euphorbiae, which has no or only a minor role as a disease vector but which can occasionally become abundant in some fields. The movement of the beneficial insects could be favored by the cutting of the crop, for example (70).

In Poland, the planting of a few rows of potato plants along the border of a field infested with CPB the previous year, as early as possible, is said to be effective in trapping the population of overwintered beetles (73). In New Brunswick, mature potato plants in pots transferred to a potato field 15 days prior to plant emergence attracted no beetles. The emerging new plants were infested immediately (Boiteau 1980, unpublished).

The planting of strips of untreated oats around potato plots tends to reduce the abundance of aphids by providing a shelter for natural enemies (59) but not necessarily to an economic level.

Field rotation:

Rotation may be a source of mortality for in-field overwinterers finding no food source at emergence. It also creates a time lag resulting in delayed population build-up in the newly planted fields. In Long Island and New Jersey, oviposition and first appearance of CPB larvae were substantially delayed in rotated fields (38 and 77). The effect of the rotation disappeared at the end of the first larval population. This was attributed to the high potential fecundity of the CPB or to the greater dispersion by flight of adults emerging in July, tending to equalize populations between fields.

Wheat was an excellent rotation crop because it acted as a barrier to CPB ground dispersal (8 h/3 m vs 2.5 h/3 m on bare soil) and, by retarding soil warming, reduced CPB flight opportunities (38). Wheat is a low value crop. The requirements of the rotation crop must not foster other problems (e.g. common scab if pH is raised) (77). More appropriate rotation crops need to be identified to make this a common practice to control CPB.

An effect similar to the one created by rotation can be seen on fields planted late. The effect may, however, be only apparent since the emigrating CPB may merely move to a nearby field that was planted earlier (77). Additional data on the process of field colonization was gathered in New Brunswick. Boiteau (11) used a network of early and late planted potato plots to show that overwintered beetles eventually abandon the first colonized field for late planted ones offering younger plants. Beetles staying on the first colonized field also had a 15% lower total fecundity than beetles that relocated. We suggest (Boiteau, unpublished) that overwintered beetles on plants reaching maturity become more mobile, disperse in quest of younger, more suitable plants for oviposition and are consequently arrested by later planted fields.

The data of Boiteau (11) suggest that it would be agronomically advantageous in Canada to plant fields as simultaneously as possible over a whole region to minimize the reproductive potential of CPB populations.

In the North East USA, protection against the colonizing adult beetles and their larvae is not sufficient because of the longer season. In Canada, however, the impact of rotation may be quite significant.

CPB densities in Virginia's tomato fields were higher in conventional-till than in no-till plots in both rotated and non-rotated fields (Zehnder et al., unpublished [ESA, Eastern 1986]).

The effect of crop rotations on the populations of predators in the potato field have not been studied. Populations might possibly be left at higher densities by some of the crops available.

Effect of weeds:

Early overwintered adult colonizing beetles were found to prefer weed-free plots (11). It is possibly best explained by the better contrast of the plant against the soil background. It may be akin to the highly successful colonization of volunteer plants.

Solanaceous plants such as the hairy nightshade, Solanum sarrachoides Sendt., can serve as reservoirs of CPB. Even though these weed hosts seem to generally retard development and often decrease fecundity, their overall importance in the determination of population levels on S. tuberosum should not be underestimated until a more detailed knowledge has been obtained (15).

Weeds can serve as reservoirs of aphids and diseases. It is important to control them in fields and border areas. Some of the common weeds hosting potato colonizing aphids are lambsquarters (Chenopodium album L.), yellow mustard (Brassica campestris L.) and redroot pigweed (Amaranthus retroflexus L.) (see Singh, these Proceedings).

Agronomic practices:

The growth of a healthy crop is another way of minimizing crop losses by insect pests. Field observations have indicated that plant vigor may play a role in non-preference by the CPB (Jermy, T., Unpublished). Vigorously growing plants tend to be less attacked than weak (Jermy, unpublished) or diseased plants (12).

The role of N treatments in pest management is controversial. On potatoes, in Pennsylvania, Jansson and Smilowitz (33) could not find any significant relation between the population parameters of CPB and 5 different rates of nitrogen. Jansson and Smilowitz (34) observed a trend for more beetles on long and very long season varieties and a significant correlation between the total seasonal abundance of the CPB and the period of time the plants required to reach maturity. Their data suggest that any agronomic factors, including the choice of the variety, that might shorten the length of time a cultivar remains suitable for feeding and oviposition should have a positive impact on pest control. They also (35) could not find a significant relation between the abundance of M. persicae and 4 different rates of nitrogen. Harrewijn (28), in the Netherlands, demonstrated on soilless potato cultures that N, P and Mg stimulated growth and reproduction of M. persicae and that certain levels of K could reduce them. The author claims he can reduce the field population of M. persicae and the number of winged forms by manipulating the supply of mineral elements. However, M. persicae being especially sensitive to the physiological conditions of its host plant, this may not be applicable to our other North American vector, the buckthorn aphid.

Insecticides:

Insecticides reduce the number and effectiveness of insect predators (8). In a ten year study, Shands et al. (62) found mobile stages of arthropod predators in only about 56% as many plants in the treated than in the untreated plantings.

A careful selection of insecticides less toxic to the predator of interest can help alleviate the problem. Lecrone and Smilowitz (39) found that C. maculata, a commonly found predator on potatoes in Pennsylvania, was more tolerant to pirimicarb than the GPA. Carbaryl and methamidophos were more toxic to the predator than to the aphids.

In Poland, Galecka (24) observed that populations of Aphis nasturtii Kalt. were smaller in potato fields located near woodlands, where the predators appeared earlier and in larger numbers, than in fields located in unwooded areas. Coccinellidae were the most abundant and permanent predators monitored (Carabidae were not sampled).

The application of the insecticide can also be made to minimize toxicity to the predator. The toxicity of insecticides used against the CPB for P. bioculatus depends on the mode of application and the stage of development of the predator. In their studies, Wegorek and Pruszynski (74) found that direct spray always caused greater losses of predators than through feeding of treated CPB larvae. Carbaryl and propoxur were the most toxic and Despirol (Kelevan), chlorfenvinphos and phosalone were the least toxic.

Chrysopa carnea is highly tolerant of many pyrethroids, microbials, growth regulators, etc., but highly susceptible to most carbamate and organophosphate insecticides (27). The existence of geographically resistant strains suggests that selection for insecticide resistant strains may be possible (27).

RESEARCH EFFORT

Information on research efforts in Canada on the use of predators to control insect pests is usually included under biological control. According to a 1985 repertory (2) of 50 researchers devoting some of their time to agricultural biological control, only one (this author) deals with potatoes in a significant proportion of his time (Table 4). A few others, in systematics and in regulatory functions, are occasionally involved in potato work but have no projects as such. Of 27 provincial and university researchers, only 2 were listed for potatoes. One works on parasites and the other one has since moved elsewhere.

No statistics are available on cultural control. From this short review, it is, however, evident that only 2-3 individuals have any significant projects involving cultural control.

Table 4. Biological control workers in Canada

	Potato	Other crops
Agriculture Canada	1	49*
Provinces, universities	2	25

*Includes people in systematics and in regulatory functions that have only occasional projects in biological control.

CONCLUSION

Predators of potato insect pests belong essentially to 4 orders and 13 families of insects and the Araneida. Very few species of predators on potatoes have been studied extensively and none of them have shown great promise.

Classical biological control is based on the use of an ideal predator that tracks the abundance of its prey. This is density dependent predation classically affected by the feeding and hunting behavior of the predator (the functional response) and densities (the numerical response). The ideal predator has a high degree of prey specificity. Few predators on potatoes are specific. Most are generalist feeders that attack prey relative to the rate of encounter. Can these generalist predators demonstrate density-dependent responses to changes in prey densities? Riechert and Lockley (55) demonstrate that this is possible for spiders. However, it seems that inter- and intraspecific competition and the frequent disruptions of the habitat in row crops like potatoes limit severely the role that spiders and other generalist predators can play in pest control.

Also, against the parthenogenetically reproducing aphids, the natural populations of sexually reproducing predators are at a major disadvantage (3). The reproductive capacity of the aphids would have to be decreased by manipulating the crop agronomically or otherwise to make them more vulnerable to predators. However, their importance should not be underestimated. Together with other natural enemies, predators complement other control measures in the field and reduce the number of migrants developing on overwintering hosts (16). The lack of endemic natural enemies and cultural controls are generally considered two of the most important factors contributing to the pest status of the

Colorado potato beetle (CPB). It might be possible to use releases of predators or other augmentative techniques to increase their impact on the beetles but this does not seem economically feasible. The introduction of predators specific to the genus Leptinotarsa from South America is being considered in the United States. Preliminary results with Pentatomidae are not encouraging but predatory mites seem to have more potential. Fortunately for Canadian producers, the single generation of CPB renders the use of simple cultural methods such as rotations more promising than south of the border.

The significance of predators and cultural methods lies not in any potential as replacements for insecticides but in their usefulness as adjunct control strategies to be protected and enhanced. In the near future, cultural methods and predators, especially the latter, will make only limited contributions to potato pest control. The low number of workers, and especially, the lack of medium to long term projects in these specialties prevent the actualization of their potential.

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THE POTENTIAL OF PLANT RESISTANCE FOR INSECT CONTROL

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ABSTRACT

The Colorado potato bettle, the potato leafhopper and several aphid species are important pests of potatoes in Canada. Cultivated potatoes are generally susceptible to these pests but high levels of resistance are present in related wild species. Glandular trichomes provide an elaborate physicochemical defense mechanism against all these pests and an enzymic browning assay is a practical screening technique. Trichomes from Solanum berthaultii Hawkes have been successfully introduced into advanced breeding selections. However, a recent report that the Colorado potato beetle can adapt to the trichomes is a warning that the development of this type of resistance must be carried out with caution. Glycoalkaloids in some species are a potential source of resistance to the Colorado potato beetle and potato leafhopper, but glycoalkaloids are unacceptable in potato tubers, and screening methods are limited. The rapid progress currently being made in understanding potato resistance to these pests suggests that variety resistance can be a practical breeding goal.

RÉSUMÉ

Le doryphore de la pomme de terre, la cicadelle de la pomme de terre et plusieurs espèces de pucerons s'attaquent à la pomme de terre au Canada. Les variétés de pommes de terre cultivées sont généralement susceptibles à ces insectes nuisibles mais plusieurs espèces sauvages voisines possèdent des niveaux importants de résistance. Les trichomes glandulaires constituent un méchanisme de défence physicochimique, complexe contre tous ces insectes. Un essai enzymatique permet de détecter la présence des trichomes glandulaires pendant la sélection variétale. Les trichomes de Solanum berthaultii Hawkes ont déjà été introduits avec succès dans des sélections avancées de pommes de terre. Le développement de ce type de résistance doit cependant se faire avec prudence car une étude récente démontra que le doryphore de la pomme de terre peut s'adapter aux trichomes. Les glycoalcaloides présents dans certaines espèces sont une autre source possible de résistance contre le doryphore et la cicadelle de la pomme de terre. Malheureusement, les glycoalcaloides sont inacceptables au niveau des tubercules et les méthodes de détection lors de la sélection des plants sont limitées. L'augmentation rapide de notre compréhension de la résistance de la pomme de terre à ces insectes nuisibles suggère que la résistance variétale peut être un objectif pratique pour les généticiens des cultures.

INTRODUCTION

Arthropod pest resistance has not yet made an impact on the cultivated potato, Solanum tuberosum L. Arthropod pest resistance is not discussed in potato breeding texts, and texts on breeding for pest resistance do not include examples from potatoes. When potato pest resistance is considered it is invariably resistance to the cyst nematodes where there have been major achievements in developing resistant varieties.

However, in the past 15 years, commencing with the observations of Gibson (18) on the effectiveness of the glandular hairs in several Solanum species in controlling aphids, pest resistance breeding has undergone a revival. In the last several years the large potato germplasm collection of the United States Department of Agriculture, the Inter-Regional Potato Introduction (IR-I) Project, has included resistance to several pests in screening its whole collection for a number of priority traits.

For the plant breeder the need to add a pest resistance to the list of traits to be selected has to be considered carefully. Potato breeding has a built in lead time of 12 to 15 years so a decision on whether to add a new trait, and if so how, depends on many factors. Since these factors determine the breeder's approach to the question it is useful to consider them before reviewing the individual pests.

Firstly, if the pest is minor, occurs only locally and is not persistent, there is no need for information about plant resistance, and there is no more to be said.

Secondly, if the pest is widespread and will frequently cause low levels of damage such that there is need for control, it is desirable to know the relative levels of resistance of the available varieties. This can be achieved by testing only the most advanced selections and including information on their resistance in the variety description so that it can be incorporated into the management of the new variety.

Thirdly, if the pest is a major problem to the extent that resistance greater than that available in present varieties and breeding material is desirable, then a whole new set of considerations comes into play. What level of resistance is required to be of economic benefit, either with resistance as the only control, or with resistance as a component of an integrated pest management program? What is the source of resistance? Is the biology of the pest such that the resistance will stand for a reasonable length of time? Is there a suitable screening procedure that can be applied to large numbers of seedlings at an early stage in the selection process and that correlates well with field performance? Is there knowledge of the genetics of resistance so that resistance genes can be moved efficiently? Are there the necessary resources, and is there the will, for breeders, entomologists and other specialists whose input is needed, to be able to work together to achieve their objective?

In this review of three potato pests, I refer briefly to their biology, many aspects of which are reviewed in other chapters in this volume, and I consider sources of resistance and resistance mechanisms, screening methods, and what may be possible by resistance breeding. I conclude by considering in more detail what is involved in incorporating resistance in a potato breeding program.

COLORADO POTATO BEETLE

The Pest

The Colorado potato beetle, Leptinotarsa decemlineata (Say), is indigenous to southern Mexico. From there it spread slowly to the foothills of the Rocky Mountains and following its adaptation to the cultivated potato it has, since 1860, spread rapidly to the rest of North America (31). Its success results from its considerable genetic variation as seen in its adaptation to the cultivated potato, the eggplant, and to less acceptable hosts, and its adaptation to drier and colder seasons in more northern latitudes (31). Contributing factors to the aggressiveness of this pest have been the ease of transport through human activities and agricultural produce, the strong flight that gives potential wide dispersal, and the apparent ease of hybridization between different populations.

These characteristics have enabled the Colorado potato beetle to develop resistance to all classes of insecticides used in a control battle that has been going on for over 100 years (17). Already the Colorado potato beetle is showing resistance to pyrethroids just a few years after their first use (15). In Canada the Colorado potato beetle has apparently been quite well controlled by pesticides until the past five or six years. During the 1980's there have been increases in the number of fields infested, increases in beetle populations, and increasing difficulties in controlling the beetles with the pesticides available (30), though these changes are probably taking place more slowly than those further south (Boiteau, pers. com.). This behaviour makes the Colorado potato beetle a major pest in many potato growing areas, and arguably the major agricultural pest in north east America (15).

In such a situation all approaches, including plant resistance, are needed to maintain a pest control capability. Reviewing recent developments Dimock and Tingey (11) suggest "the time is ripe for the development of plant resistance" to this pest. What are the prospects?

Resistance Sources and Mechanisms

It is generally considered that S. tuberosum Group Tuberosum is susceptible to the Colorado potato beetle although there are small differences among varieties (11). The primitive cultivated potato S. tuberosum Group Andigena is also susceptible (64). However, it should be noted that even in susceptible varieties plant response to pest damage is modified by physiological factors that control plant vigour, tuberization and bulking rates (13). These are also traits considered by breeders as they select clones with desirable foliage type and yield components. For example rapid bulking characteristics permit some flexibility in crop management such that adjustment of planting dates may enable the crop to develop out of phase with the peak pest population, so avoiding the time of greatest damage. This is being applied in Rhode Island with the Fredericton bred variety Caribe (7).

In contrast to the cultivated potatoes there is considerable resistance in the wild tuber-bearing Solanum species. This was first recognized in 1950 by Torka (82) who also established a link between plant resistance and glycoalkaloid levels. Kuhn and Low (32) and more recently Sinden et al. (65) have demonstrated that different alkaloids have different affects on plant resistance. The glycoalkaloid-resistance link resulted in S. chacoense Bitt. and S. demissum Lindl. becoming the basis for resistance breeding in several European programs (50). Many of the subsequent studies on sensory physiology, host selection, feeding behaviour and metabolism have been cited in recent reviews (11, 66, 73). Recent studies in Maine (37) have also shown that Colorado potato beetles reared on S. chacoense and S. demissum have protracted development times, are smaller and have higher mortality than beetles raised on the variety Katahdin.

A different resistance mechanism was identified by Gibson (21) when he described the effectiveness of glandular trichomes in reducing Colorado potato beetle damage by entrapment with a sticky material produced by S. polyadenium Greenm. Gibson & Turner (24) went on to describe short, 4-lobed type A hairs on S. polyadenium, S. berthaultii and S. tarijense Hawkes, and longer type B hairs with sticky drops at their tips on S. berthaultii. Ochoa (39) reported similar glandular trichomes in S. x flavoviridens Ochoa, while Tingey et al. (78) added another four species. The resistance in S. neocardenasii Hawkes & Hjerting does not appear to be related to glandular trichomes (12). The manner in which the exudate is released from type A trichomes and is then oxidized to a hard brown substance that encases insect tarsi has been described by Ryan et al. (51), and the interaction of the combined A and B type trichomes in a physicochemical insect defense mechanism elaborated in detail by Gregory et al. (26).

The adverse effects of the glandular trichomes of S. berthaultii on population dynamics of Colorado potato beetle have been investigated (6, 84). However, not all of the resistance in S. berthaultii is conferred by the sticky exudate. Studies on the mechanism of feeding deterrence of compounds produced by the B type trichomes are currently underway by Pelletier and King (40). While glandular trichomes appear to hold considerable promise as a resistance mechanism, Groden and Casagrande (27) have recently shown the Colorado potato beetle to adapt rapidly to the resistance of S. berthaultii. Clearly it is important to learn as much as possible about the nature of this resistance so that its use can be optimized.

In the past few years the Inter-Regional Potato Introduction Project (29) of the U.S.D.A. has been able to screen most of its large collection of potato species for resistance to the Colorado potato beetle. Resistance far greater than that in present varieties occurs in the Mexican species S. pinnatisectum Dun. S. trifidum Corr. and S. polyadenium, and in the South American species S. chacoense, S. tarijense, S. berthaultii and S. capsicibaccatum Card. (47, 48, 56). Only three of these species have glandular trichomes.

Screening Methods

Screening methods have been reviewed by Sanford et al. (59). Much of the resistance screening has been carried out in the field with natural infestations, counts of egg masses, larvae and adults to estimate infestation levels and visual scores to estimate foliage damage. In some cases artificial infestation of plants or plant parts has been used. Such methods usually limit the numbers that can be tested because of the work involved. This restriction makes such methods unsuitable for the early generation selection work that is necessary for a program where resistance breeding has a high priority.

The various methods available for measuring total glycoalkaloid levels and individual glycoalkaloid composition have been reviewed by Coxon (8) but with the exception of the new immunoassay techniques for total glycoalkaloids they are not suitable for routine incorporation into a breeding program (25). Glandular trichomes can be evaluated by an enzymic browning assay (3).

Breeding

As happens in so many instances the resistance developed in the European programs from S. chacoense and S. demissum dropped off as backcrosses were made to Group Tuberosum types to improve other characteristics (50). This failure is the result of several factors (11, 73). Firstly, the polygenic control of total glycoalkaloids makes the breeding work more complicated (60). Secondly, there is a high correlation between total glycoalkaloid levels in foliage and tubers (10). Thirdly, there is a compounding influence of environmental effects and the possibility of the synthesis of novel alkaloids depending on the specific genotype of the parents (66).

On the other hand, the differential activity of specific glycoalkaloids may be worth investigating further. Leptine, for example, has an extremely high level of activity (69) and is reported to be found in foliage but not in tubers (65), and clones with commersonine and dehydrocommersonine are significantly more resistant than clones with other glycoalkaloids (65). Tomatine acts as a repellant while demissine acts as a feeding deterrent (4). Additional requirements for such an approach are a rapid and efficient screening procedure, as well as mammalian toxicity studies on the less familiar glycoalkaloids.

In contrast, glandular trichomes may be an attractive resistance mechanism, since the beetle is less likely to counteradapt to physical entrapment than it is to adapt to a metabolic toxin or inhibitor (11, 72). As knowledge of the inheritance of the glandular trichomes has increased it has been determined that inheritance is quantitative rather than simple in nature (35). Breeding for Colorado potato beetle resistance based on S. berthaultii was commenced at Cornell University in New York State in 1977 (11), and progress has been made in moving this resistance into advanced hybrids (84). Selection for resistance should benefit from the use of the improved screening method developed by Ave et al. (3). However, as already noted above, caution is necessary following the recent report that beetle populations can adapt to S. berthaultii (27).

THE POTATO LEAFHOPPER

The Pest

The potato leafhopper, Emposasca fabae (Harris), has long been recognized as an important potato pest and in the 1940s it was considered to be one of the most destructive potato pests in the United States at least in some of the midwest States (68). Yield losses from this pest can be considerable, though there is not necessarily a correlation between infestation levels, hopperburn injury, and yield loss (63). In Canada leafhopper damage is not widespread, but it is a common pest in Ontario where injury and hopperburn can be locally severe.

The importance of this pest led to the establishment in 1934 of a program to breed for resistance (68). The results of this work are reviewed in two recent papers (42, 59). At least one leafhopper resistant variety, Sequoia, was released at this time (16), though the original cross and early selection took place before the pest resistance breeding program came into being.

In the 1970's the interest in the potato leafhopper in the U.S. increased again, especially in Sanford's group at Beltsville, and more recently in Tingey's group at Cornell.

Resistance Sources and Mechanisms

The varying levels of resistance among conventional S. tuberosum Group Tuberosum breeding material is described in recent reviews (42, 59). However, the foliage resistance in this material is not great, and is of limited value without additional pest control measures (63).

Some resistance is reported in the primitive cultivated Group Andigena of S. tuberosum (64, 79). Resistance of a greater order of magnitude is present in some of the wild tuber bearing Solanum species. One of the earliest reports of such resistance is by Sleesman (67) in 1940 who found S. polyadenium to be higly resistant, if not immune, and S. chacoense and S. commersonii Dun. to be highly resistant. Radcliffe and Lauer (43) reported an extensive evaluation of many species from the IR-1 collection and found that representatives from 35 species had a level of resistance that did not differ significantly from immunity. More recently, further evaluation of the same collection by Flanders & Radcliffe (14) identified resistance in nine species, seven of which were resistant species also found by Radcliffe and Lauer (43).

Nymphal infestations of potato leafhopper were found to be highly correlated with total foliar glycoalkaloids in ten species studied by Tingey et al. (77). This result was confirmed by further studies on leafhopper feeding and survival on the same species by Raman et al. (49), and in S. pampasense Hawkes and S. tuberosum by van de Klasharst and Tingey (83). Further evidence of a causal role for glycoalkaloids in potato leafhopper resistance was provided by Tingey (72). However, both Tingey et al. (77) and Raman et al. (49) noted that there were probably also effects from quantitative differences in individual glycoalkaloids. Dahlman and Hibbs (9) found that among several extracts of alkaloids from *S. chacoense* some restricted feeding and caused mortality, while others were a deterrent but did not affect survival.

In some instances the resistance is caused by mechanisms other than alkaloids. Tingey and Gibson (74) were the first to demonstrate that resistance to potato leafhopper in *S. berthaultii* and *S. polyadenium* was the result of the immobilising exudate from the glandular trichomes which impaired feeding and mobility. Further studies showed that the presence of both type A and B trichomes resulted in a greater level of resistance than if only type A trichomes were present (81). The effectiveness of glandular trichomes as a resistance mechanism was demonstrated by *S. berthaultii* hybrids with trichomes in which leafhopper populations were reduced 80% compared with commercial cultivars (76).

Screening Methods

As in so many other situations, screening for resistance to the potato leafhopper has to take account of large environmental variances (61) and host plant age (55). Whole plant testing using small field plots and a minimum of replication was found to be feasible by Sanford and Sleesman (62). The results from such tests have to be interpreted with caution, however, since plants which support small infestations and are classified as resistant when evaluated in mixed populations may support relatively higher infestations when grown in isolated blocks (59). Nevertheless, relative differences among selections are maintained in such situations.

Several alternative approaches to field plot evaluation have been attempted. Sanford et al. (57) compared oviposition on detached leaves with field nymph infestation densities and found similar rankings at the extremes of the resistance range. Van de Klasharst and Tingey (83) used a glasshouse seedling stage evaluation and concluded that it was satisfactory but suggested that it should supplement rather than replace field screening. These methods have the advantage that they can be applied to large populations without the need to multiply stocks which makes them suitable for use in early generation selection, especially in the development of new resistant parental material. However, such methods require that the resistance of survivors be confirmed in whole plant field tests.

Laboratory evaluations are possible for glycoalkaloid analysis and have been reviewed by Coxon (8). The limitations noted above in relation to the Colorado potato beetle apply here also. Glandular trichomes can again be evaluated using the browning bioassay of Ave et al. (3).

Breeding

Sanford and Sleesman (61) found the genetic variance for potato leafhopper resistance to be mostly non-additive, and predicted slow progress in selection. Later they found only a low heritability for resistance to leafhopper in Group Tuberosum material: heritabilities ranged from 23 to 52% with a mean of 36% (62). Nevertheless they commenced a program of phenotypic recurrent selection and after five cycles of selection had achieved a 57% decrease in infestation levels (58).

Resistance breeding based on the immobilizing exudate from the glandular trichomes would proceed as described for Colorado potato beetle above.

APHIDS

The Pest

Aphid numbers themselves have not been a problem since pesticide control became available, but they are a considerable problem as vectors of several virus diseases that cause yield losses and problems in seed production.

The possibility of aphid resistance having any impact on transmission of non-persistent viruses seems remote, and it is reasonable to expect this problem to be solved best by the development of varieties with resistance or immunity to PVY and other non-persistent viruses. However, transmission of persistent viruses takes some time, and requires a period of aphid feeding. In this situation there is potential value for mechanisms of feeding deterrence. Since high levels of resistance to the main persistent virus, PLRV, are not available, or may only be available from non-tuber bearing *Solanum* species with difficulty, it may be worthwhile pursuing resistance to aphids as a factor in PLRV control.

Resistance Sources and Mechanisms

There are antibiotic types of resistance in varietal material (5), and there is resistance within the primitive cultivated material of Group Andigena (79). However, as with the other pests the greatest levels of resistance are to be found in the related wild species. The first studies were reported by Adams (1) in 1946 and more recently Radcliffe and his colleagues have conducted extensive testing (44, 45). In their studies Radcliffe and Lauer (44) noted plant resistance to *M. persicae* (Sulzer) and *M. euphorbiae* (Thomas) is generally positively correlated though there are exceptions. Gibson (19), studying three *Solanum* species and three aphid species, found the resistance of each *Solanum* species differed with the aphid species, the part of the plant, and the condition of the leaf.

Again, the glandular trichomes in several species provide an effective resistance mechanism. This source of resistance in *S. berthaultii*, *S. tarijense* and *S. polyadenium* has been studied by several authors (18, 20, 33, 75), and similar resistance in *S. neocardenasii* has been studied by LaPointe and Tingey (34). To these Ochoa (39) adds *S. x flavoviridens* though this has not been studied in detail. This resistance in *S. berthaultii* and *S. neocardenasii* is associated with high levels of polyphenol oxidase (52) and the presence of B type trichomes (33, 34). Another characteristic of *S. berthaultii* that appears to contribute to its aphid resistance is the release of an aphid alarm pheromone from the B type trichomes (23).

Other resistant species do not have these glandular trichomes. Further, Radcliffe (42) has noted that glycoalkaloids do not appear to be involved in resistance to aphids. Another approach to understanding plant resistance to aphids is the electrophysiological monitoring of probing and feeding behaviour (2, 70). This shows the operation of more than a single mechanism of nonpreference since successful proboscal contact, penetration and feeding requires several distinct steps that offer the possibility for multiple gene control and a durable, nonpreference type of resistance (71).

Screening Methods

Screening methods for evaluating aphid resistance have been reviewed by Sanford et al. (59). Most of the work on evaluating resistance to aphids has been conducted with field plots or caged plants, and has estimated rates of aphid growth and population increase. Although Radcliffe et al. (46) found aphid resistance to be relatively stable in field tests of species germplasm over several environments, reliable results require several environments and several aphid counts. These methods are therefore useful for preliminary evaluation if no replication is used, or for a final estimate of resistance if resources permit replication and much more aphid counting.

An alternative method of evaluation is the use of excised leaflets. Sams et al. (53) found field tests and excised leaflet tests with M. persicae to be correlated at the 1% level of significance and concluded that the excised leaflet test was suitable for the preliminary assessment of resistance. In material in which the resistance is based on glandular trichomes, an enzymic browning assay (3, 52) provides a practical method of screening for trichome activity.

The electrophysiological monitoring of aphid feeding behaviour as a screening technique has been reviewed by Tarn and Adams (71). While the method facilitates selection for high levels of resistance and enhances understanding of the type of resistance, it is not adapted to handle large numbers of selections at the early stages of a breeding program.

Breeding

The heritability of resistance to M. persicae was estimated at 72% in field experiments with a wide range of potato germplasm (46), and at 50-60% using excised leaflets to evaluate hybrid progenies involving wild species and cultivated selections (54). This work indicates progress in transfering resistance from wild species into the cultivated material of variety development programs.

The heritability of glandular trichomes in S. berthaultii and S. tarijense was at first thought to be relatively simple (22). However, studies by Mehlenbacher et al. (35, 36) in S. berthaultii and hybrid progenies indicate that resistance is probably the result of the interaction of several chemical and physical characteristics of the glandular trichomes, and that inheritance is effectively quantitative. Aphid population reductions caused by glandular trichomes have been maintained in field evaluations of F3 hybrids of S. tuberosum x S. berthaultii (80), and since glandular trichomes appear to be a more important resistance factor than glycoalkaloids (81) it should be possible to develop resistant cultivars with the normal low glycoalkaloid levels.

INCORPORATING RESISTANCE IN A BREEDING PROGRAM

At the outset I posed a number of questions to be answered before undertaking a program to breed for potato resistance to insect pests. I have discussed some of the relevant information for three pests. I wish to conclude by looking in more detail at the impact on a breeding program of introducing a new characteristic where there may already be 70 traits under evaluation and selection.

Although our knowledge is steadily increasing there is still a vast amount that we do not know. At the level at which the pest is responding to stimuli to feed or not to feed we know very little, and certainly not sufficient to select a specific component of the plant-insect interaction as the basis for resistance breeding. Electronic monitoring of feeding provides valuable information on aphid behaviour, and an understanding of resistance mechanisms (33, 34, 71) but is not a practical screening method. Glycoalkaloids provide a potential resistance mechanism against Colorado potato beetles and potato leafhoppers, but are not involved in aphid resistance. They include chemicals with valuable resistance attributes, for example the leptines (69), but there are potential problems with unacceptable levels of glycoalkaloids in tubers. Research on glandular trichomes has shown them to provide an elaborate physicochemical defense mechanism (23, 26). This appears to be effective for aphid control in field situations and to be compatible with beneficial insects (38). It has even been suggested that the trichomes may contribute to controlling the spread of non-persistent viruses (28). Since this resistance has been considered to be durable the recent finding that the colorado potato beetle has the potential to adapt quickly to the trichomes (27) is cause for caution.

We have seen throughout that the highest levels of resistance are in wild species related to the cultivated potatoes. If a breeding program is to utilize resistance genes from such germplasm they must be introduced at the variety level without introducing unacceptable traits such as late maturity and high glycoalkaloids. This normally requires several cycles of crossing, evaluation and selection to develop acceptable parental clones. The task of accessing this germplasm is becoming easier as our knowledge of haploids, unreduced gametes, and endosperm balance numbers enables us to overcome most of the crossing barriers among potato species (41). The development of parental clones incorporating new traits may take a minimum of five years, depending on the species used, the trait and selection method.

Once parents are available, and progeny are created which are segregating for the new trait as well as for quality, yield and all the other important traits, a suitable screening method is still required.

If the trait is assigned a high priority and screening is carried out at an early stage in the program, it is necessary to have an evaluation procedure that can handle hundreds or even thousands of individuals. Alternatively and with a lower level of priority, at later stages of the selection program when only the superior selections remain, evaluation for insect resistance may only involve dozens of clones.

Last, but by no means least, when all these pieces have been put together it is necessary to state what every other author says - that it is essential to have good teamwork involving breeders, entomologists, and if necessary other disciplines, plus adequate resources for screening, to make it all work.

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CONTROL OF BACTERIAL RING ROT

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ABSTRACT

Bacterial ring rot (*Corynebacterium sepedonicum*) is a serious disease of potato. Symptomless infections, which often develop with this disease, are of particular concern because the causal bacterium can spread from such infections to other tubers and tuber lots without being detected. Since the potato tuber itself is the major inoculum source and symptomless infections can now be detected in laboratory tests, ring rot control through eradication of the disease may be feasible. However, it is uncertain whether the pathogen can be eradicated entirely. Adequate research on the ecology and other possible inoculum sources of *C. sepedonicum* has not yet been done. In practice, eradication of the disease would involve reducing inoculum and preventing dissemination of any inoculilm that may be present.

RESUME

La flétrissure bactérienne (*Corynebacterium spedonicum*) est une maladie très sérieuse de la pomme de terre. Les infections sans symptomes qui se developpent fréquemment chez cette maladie sont particulièrement dangereuses. La bactérie peut se propager à partir de ces infections aux autres tubercules sans être detectée. Puisque le tubercule lui-même est la source majeure d'inoculum et puisque les infections sans symptômes peuvent maintenant être détectées par des tests de laboratoire, le controle de la flétrissure par des test de laboratoire, le controle de la fletrissure par éradication est maintenant possible. Nous ne savons cependant pas encore si le pathogène peut être éradiqué entièrement. Il faudra plus de recherche sur l'écologie et les autres sources possibles d'inoculum. En pratique, l'éradiation de la maladie impliquerait la reduction de l'inoculum et la prévention de la dissémination de tout inoculum presént.

INTRODUCTION

The bacterial ring rot disease of potato was found in Canada 20 years after it was first described in Germany in 1910. The causal organism is *Corynebacterium sepedonicum* (Spieck. & Kotth.) Skapt. & Burkh. Other names for the organism, such as *Clavibacter michiganense* subsp. *sepedonicum*, have been suggested recently to reflect current insight into its taxonomic status but the familiar *C. sepedonicum* designation will be used in this treatise.

The bacterium is a Gram positive, slightly club-shaped pleomorphic rod (c. 0.5 x 1.0 um) that often appears in L or V formations. Under some conditions, coccoid forms have been observed *in planta* and in culture but revert to short rods after subculturing. In culture, colonies are usually mucoid when first isolated but non-mucoid colony types frequently occur in older cultures. In two reported instances, non-mucoid colony types have been isolated directly from diseased plants.

Corynebacterium sepedonicum has not been very well characterized with regard to biochemical and physiological characteristics and is therefore difficult to identify without pathogenicity tests. It is similar to other Gram-positive, plant pathogenic bacteria such as the agents of bacterial canker of tomato (*C. michiganense*) and alfalfa bacterial wilt (*C. insidiosum*).

DISEASE EXPRESSION

Bacterial ring rot symptoms typically appear on potato foliage near the end of the growing season. First symptoms usually occur on the lower leaves as slight rolling of the margins and loss of turgidity. Affected leaves become pale green and droop. Regions between the veins lose color and progress from pale green through pale yellow before beginning to die and turn brown. Eventually, all leaflets die and the leaf drops off. Symptoms usually progress upwards in the stem and may affect only one or all stems of the plant. Some potato cultivars occasionally express a rosetting symptom, characterized by short stem internodes and an upright plant habit, early in the growing season.

In tubers, the earliest symptoms are a slight yellowing and softening in the vascular ring. As the disease progresses, softening in the vascular ring becomes more pronounced and when pressure is applied from the outside, an exudate with cheese-like texture emerges from the xylem vessels. Subsequently, the outer cortex may become separated from the inner cortex. Also, reddish brown discoloration may develop directly under the periderm and surface cracks may develop. In advanced stages of disease, secondary microorganisms often proliferate in the affected tissue, masking typical symptoms.

The development of symptoms is affected by a number of factors including cultivar characteristics, environmental growing conditions, and the presence of other potato pathogens. Some cultivars develop symptoms more readily than others at the same level of infection. In fact, some cultivars like Teton only very seldom exhibit ring rot symptoms although they are susceptible to infection. Other cultivars such as Red Pontiac and Bintje express symptoms readily under a wide range of growing conditions. All cultivars, however, can harbor symptomless infections in which the pathogenic bacteria are present without disease expression.

Generally, symptoms are expressed most readily in plants that have lush foliage and are then subjected to stress. Symptom development is accelerated under warm weather conditions when plants undergo moisture stress, whereas in cool weather, symptoms may be delayed or fail to develop altogether. Some evidence suggests that ring rot develops more slowly under dry than under wet soil conditions. Dykstra (8) reported this difference between irrigated and dryland plots. The effect has also been observed between dry and moist growing seasons (5).

In the more northern potato growing regions where the number of degree-days and mean temperatures are low and the photoperiod is long, symptoms appear to develop slower than in the southern areas (24). Nelson and Kozub (21) also found that disease severity was greater under short (8-12 h) than under long (16 h) photoperiods. They suggested that these results may explain why symptoms are often not observed until late in the growing season when total light energy is lowest. Bishop and Slack (1) found that symptoms were more severe when night temperatures were maintained at 24 C than at 5 C with constant 24 C day temperatures and a 12 h photoperiod. Both cool and hot soil temperatures seem to delay symptom expression. Lodgson (13) found that more plants expressed symptoms at 25 C than at 16, 19, 22, 28, 31, and 34 C.

Whether soil fertility has an effect on bacterial ring rot is virtually unknown. One preliminary report does suggest that application of nitrogen fertilizer decreases disease expression (11). It would be expected that the effect of fertilization varies with soil type and fertility.

Disease expression may also be affected by the presence of other potato pathogens. Nelson and Torfason (22) reported that leaf roll infections mask ring rot symptoms. Similarly, potato viruses X and S were found to alter ring rot symptomology (20). In the field, the blackleg disease (caused by _Erwinia_ _carotovora_ subsp. _atroseptica_) is also often present in association with ring rot. Whether blackleg predisposes potatoes to development of ring rot symptoms or whether ring rot infection predisposes plants to the blackleg disease has not been studied.

Inoculum concentration has a significant effect on disease expression. Seed tubers inoculated with a high concentration of bacteria develop more symptomatic plants than those inoculated with a low concentration. With low inoculum levels, however, symptomless infections do occur (25). Sletten (28) also reported that symptomless infections developed in plants grown from root-inoculated stem cuttings when low inoculum levels were used. Nelson (18) found that Russet Burbank plants grown from potato tubers inoculated with 300 colony forming units (cfu) did not express symptoms but did develop symptomless infections. In contrast, plants from seed tubers inoculated with 3000 cfu or more became diseased and developed less symptomless infections.

INOCULUM SOURCES

The primary source of inoculum is infected tubers. Tubers with ring rot symptoms contain high concentrations of bacteria which are readily transferred to other potato tubers. Tubers with symptomless infections also may harbor large numbers of bacteria, although symptomless infections with very low numbers of bacteria also occur (5, 29). The potential of latent infections as an inoculum source depends to some extent on the bacterial concentration but in general they are highly significant since such infections can go undetected for several potato generations. Infected seed tubers are an especially important source of inoculum because of their close association with other seed tubers. Infected commercial or tablestock tubers probably are of less importance as an inoculum source since they can be kept physically separated from seed tubers. In the field, however, infected commercial crops could serve as inoculum sources for seed crops in close proximity.

Infected potato tubers that survive the winter in the field and grow as volunteer potato plants in subsequent growing seasons can also serve as a reservoir for ring rot inoculum. *Corynebacterium sepedonicum* can also survive in potato plant debris from one growing season to the next under some conditions (16, 19). Volunteer plants are of greatest concern when recommended crop rotation practices are not followed. Cull piles serve as a source of inoculum when infected tubers are not properly disposed of and bacteria are spread by one of several ways to healthy seed tubers.

It has often been speculated that alternate hosts may serve as a reservoir for ring rot inoculum but no evidence was available until recently. Bugbee et al (2) recovered *C. sepedonicum* from field-grown sugarbeet roots and showed that the isolates were pathogenic on potato. The relationship of sugarbeet infection to the over-all epidemiology of ring rot is not clear at present. Nevertheless, the role of other crop and/or weed species as potential hosts needs to be reassessed.

Evidence from early field experiments on ring rot suggests that the disease does not survive in soil. This conclusion is based on the observation that ring rot symptoms did not develop in plants grown in fields in which highly infected crops had been grown the previous season (9). Furthermore, *C. sepedonicum* could not be isolated from soil in tubes that had been buried in the soil overwinter (9, 30). Nelson (16) also found survival in non-sterile soil to be very short; 5-15 days as determined by a bioassay test using potato stem cuttings. However, since we know today that at low inoculum levels infected plants may not express symptoms but carry the inoculum for several generations and that the organism is very difficult to isolate from complex environments where many other microorganisms are present, the final conclusion about soil as an inoculum source seems unwarranted at this time. Although no direct evidence to suggest that it does survive in soil has been published, neither is there good evidence that it does not survive in soil at all. A re-examination of soil survival is needed.

DISSEMINATION OF INOCULUM

Man and his activities are no doubt the most important means by which *C. sepedonicum* is spread (eg. ref. 26). Contaminated equipment used on seed potatoes is the primary means by which the disease is being maintained in North America. Among the equipment being used, the seed cutter is one of the greatest culprits. The presence of an infected tuber, symptomatic or asymptomatic, in a batch of potatoes being cut will contaminate the cutting knife and rollers which will in turn transfer the bacteria to disease-free tubers. Similarly, the pick of picker-type planters can transfer the bacteria to many additional tubers once it has become contaminated. Although cutting and picker-type planting machines are the major agents of disease spread, other equipment, storage containers, and vehicles with which seed potatoes come in contact are potential agents of spread. Nelson (15, 17, 19) has shown that ring rot bacteria can survive on clothing, machinery and storage surfaces for long periods of time. The bacterium persisted on contaminated surfaces of burlap, kraft paper, and polyethylene plastic for at least 24 months at 12% relative humidity and 5 or 20 C. Survival was reduced to less than 14 months at high relative humidities (94%). This confirms other observations that Gram-positive bacteria generally survive well under dry conditions. Cold, freezing temperatures also favor bacterial survival.

It has been postulated that man may also spread the disease by various other activities which necessitate contact with seed potato crops. For example, ring rot could be spread by someone, including potato inspectors, walking from one field in which a symptomless infection is present to another. Perhaps also, repairmen that need to walk over stored potato piles could spread the disease if they contact a diseased tuber.

Insects transmit many diseases of man, animals and plants. The Colorado potato beetle, grasshoppers, tarnished plant bug, leafhoppers, and aphids have all been reported to transmit C. sepedonicum to healthy plants (7, 12). The importance of insect transmission in the field has not been evaluated but the movement of bacteria from an infected plant to neighboring plants and to adjacent fields are deemed possible on the basis of the experimental results. It has also been suggested that perhaps other animals including birds contribute to field spread.

DISEASE ERADICATION

With the current state of our knowledge, there appears to be only one effective way to control bacterial ring rot -- that is by eradication. What is meant by eradication must be carefully described, however. When a disease no longer occurs we usually think of it as having been eradicated, but if it can be shown that the disease-causing organism is still present in the environment, it can not be considered eradicated. Thus a distinction can be made between "eradication of the disease" and "eradication of the pathogen". As far as the potato industry is concerned it would seem enough to eradicate the disease, that is, to attain the situation in which bacterial ring rot never manifests itself as diseased plants. However, if the pathogen is not eradicated then practices would have to remain in effect to keep the incidence of ring rot at nil. Thus it would be advantageous to eradicate the pathogen, i.e. eliminate it entirely from Canada. Whether the pathogen can indeed be eradicated completely is difficult to evaluate at this time since our knowledge of the epidemiology and ecology of the pathogen is far from complete. Moreover, how would we know when the pathogen is eradicated? If eradication depends on the ability to detect the pathogen, then the success of eradication would be dependent on changes in technology. The better the technology for detecting the pathogen, the more difficult it would be to "eradicate" the pathogen.

When certification regulations with a zero tolerance level for the ring rot disease were first instituted some 40 years ago, it had been hoped that the disease could be eradicated. Although the regulations have kept the disease to a manageable level, it still plagues the potato industry today and the entire objective has not been achieved. Perhaps it is time to re-examine current practices in light of recent developments to determine what precisely the objective of eradication ought to be and how it can be achieved.

The concept of bacterial ring rot eradication is based, to a large extent, on the experience in Europe. Although the disease was present there at one time, it is said to no longer exist in many of the Western European countries. It is difficult to verify the exact situation in Europe but it is clear that the disease does not normally occur there. Whether the pathogen still exists in Europe is another question and recent unpublished information does perhaps suggest that the pathogen is present in Europe. It is quite possible that by their cultural practices the ring rot inoculum levels are kept so low that the disease is seldom if ever expressed in their potato crops. In light of this, is it logical for Canada to attempt total eradication of the pathogen? Perhaps using the European approach of enforcing grower practices which discourage the increase and spread of *C. sepedonicum* should be carefully considered.

In order to assess the success of keeping inoculum levels low, it is necessary to monitor the bacterial population levels in seed potatoes. Until recently the Gram stain was the only procedure that was useful for routine testing. The Gram stain, although useful for high inoculum levels where many pathogenic bacteria are present, is notoriously non-specific. Serology provides a more accurate means for specific detection of a single bacterial species. Various serological procedures can be used such as Oucherlony double diffusion (3), latex agglutination (27), and immunofluorescence (4). The specificity of serological tests is greatly enhanced by the use of monoclonal antibodies. Such antibodies, if carefully selected, are highly specific for the ring rot bacterium and provide a dimension to ring rot detection not previously attainable (5, 6).

Reducing inoculum

Any approach to bacterial ring rot eradication must deal with getting rid of inoculum sources. Even if the pathogen can not be eradicated altogether, the inoculum must be kept very low, below levels which would lead to disease expression. In the past all infected crops have been eliminated from the seed program and this practice must continue as an important aspect of any control program. Accurate field inspection, therefore, must continue to be emphasized as it is the place where the potato crop can be observed most readily. Late season inspections are valuable for detecting ring rot because symptoms tend to be expressed during the latter part of the growing season. In addition to field inspections, laboratory tests should be used to detect symptomless infections. Although the laboratory tests are time-consuming and practical difficulties in obtaining statistically significant samples exist, they provide important information as to the status of symptomless infections. Serological testing of tubers that has been done in New Brunswick and Prince Edward Island for the European market attest to their value.

The limited generation Elite program is another important aspect of bacterial ring rot control. This program assures that all pre-Elite seed originates from pathogen-free plant material and requires that all potato lots be flushed through the system. Thus if a potato lot should become contaminated with the ring rot organism somewhere between the Pre-Elite and Certified stage, and the amount of inoculum builds up in that seed lot each year, the seed lot may be passed through the seed program before the inoculum level reaches the point at which the disease is expressed. If such a seed lot cycles within the seed program for several more generations, it is almost certain that the disease will express itself sometime. Furthermore, the rejection of all seed lots on a farm where ring rot has been identified, rather than only the seed lot in which the disease was found, is a necessary precaution since the pathogen may have been spread inadvertently to other seed lots before the infection was discovered.

Since the possibility of field spread also exists, ring rot in commercial and tablestock crops is also of concern to the seed industry. This potential source of inoculum can only be eliminated through control of the disease on commercial farms. Commercial potato growers can minimize the risk of contracting the bacterial ring rot disease by planting only certified or better grade seed, as well as following sanitary agronomic practices.

Another source of inoculum is volunteer plants and potato debris. To eliminate this inoculum, field practices should be geared to prevent regrowth of tubers left in the field and to encourage rapid breakdown of potato plant tissues. Crop rotation must be adequate to ensure that all potato debris and tubers are gone before a crop of seed potatoes is planted.

Some potato cultivars express bacterial ring rot symptoms more readily than others. In Canada, only cultivars that express symptoms reasonably well may be licensed. This regulation is to minimize carry-over and cross-contamination by symptomless carriers. However, since all cultivars are potential symptomless carriers, a false sense of security may arise from reliance on this regulation. In actual fact it may be that by growing only highly susceptible cultivars, inoculum levels may increase more than they would have in tolerant cultivars and actually contribute to the amount of inoculum present. Perhaps it may be advantageous to grow more tolerant cultivars which would also decrease the frequency of disease expression. Of course, caution would have to be used to restrict spread of symptomless infections but this should also be done for susceptible cultivars since these too may be symptomless carriers.

The bacterial ring rot disease problem would not exist if good resistant cultivars were available. Resistant cultivars are those that do not permit multiplication of the pathogen in contrast to tolerant cultivars which are themselves not affected by the pathogen but do support pathogen multiplication. Effort should be made to find sources of ring rot resistance for incorporation into the genomes of important potato cultivars.

Preventing the dissemination of inoculum

Eradication of bacterial ring rot will not only require minimizing the amount of inoculum but also limiting the spread of inoculum that may be present. There has always been a great emphasis on clean-up and disinfection where bacterial ring rot has occurred or may have been contacted. This emphasis must be continued. Although disinfection practices on the farm are often difficult to execute as precisely as they should be, all attempts need to be made to ensure that inoculum is not spread by equipment, vehicles, and storage containers. Most disinfectants are inactivated by soil and organic matter and thus clean-up procedures need to be extensive. Also the length of time surfaces to be disinfected are exposed to the disinfectant must be adequate; usually 10 min is recommended but seldom attained.

In addition to disinfection, general sanitation procedures must be practiced. That means tubers should not be left lying around buildings and equipment and all cull piles should be buried.

Perhaps the greatest spread of bacterial ring rot takes place with the cutting procedure. Therefore, it is strongly advised to used whole seed pieces. It is often argued that it is not economically feasible to use whole seed since more seed pieces can be obtained from cut tubers than from whole seed on a weight basis. It should be possible, however, to use whole tubers for the highest classes of seed and cut tubers for the remaining classes. For example, whole seed could be used to plant the Elite I and II classes where acreage is relatively small and then cut seed used for the Elite III and lower classes where acreage is much larger. Large tubers in Elite I and II seed which are unsuitable for planting without cutting could be downgraded to Elite III. By use of whole seed, the possibility of introducing the ring rot pathogen by cutting is removed. If the pathogen where to be introduced at a later stage in the seed increase program, chances are that the inoculum would not build up to the point that symptoms are expressed before it has been flushed out of the seed program.

If whole seed is used, of course it is also necessary to avoid the use of picker-type planters since these also transmit the bacterium among tubers the same way as cutting knives do.

In order to control bacterial ring rot, or rather to prevent ring rot from occurring on a seed potato farm, the grower must take all precautions to prevent contact with an inoculum source. That means equipment used for a commercial crop must not be used for the seed crop. Also storages must remain well separated. Ideally, commercial potatoes should not be produced on farm operations on which seed potatoes are produced. Furthermore, precautions must be taken that individuals, who come in touch with seed potatoes, have been adequately disinfected or have not had any contact with other potato crops.

FUTURE OUTLOOK

Control of bacterial ring rot is increasingly becoming a major concern of the potato industry in both Canada and the United States. In Canada the increasing concern is largely due to pressures from countries that import seed potatoes. In the U.S. concern has resulted from litigation over the disease which has been frequent and costly. However, there has also been direct concern on the part of individual seed potato growers -- might they contract the disease despite all efforts to avoid it?

Research has been slow in coming up with answers to questions that have been raised. This is due in part to the relatively small number of scientists working on the disease, but also in part due to the difficulty in working with the organism. *Corynebacterium sepedonicum* is particularly difficult to isolate and study.

Biological data on coryneform bacteria in general is limited and the ring rot organism especially does not lend itself well to standard microbiological techniques. Also the disease is difficult to study. Symptoms occur erratically and the source of the pathogen in disease outbreaks frequently cannot be traced.

It has been recognized for a long time that symptomless infections are a major source of the ring rot problem. The pathogen may have been spread far and wide before the source of infection is discovered. Consequently, recent research efforts have been made in the area of symptom expression. What are the factors that determine whether symptoms will be expressed? Under what conditions do symptomless infections propagate themselves for one generation after another? Answers to these questions will help field inspectors to recognize conditions and cultivars that hamper their ability to detect the disease at an early stage.

Early detection of infections is also increasingly becoming possible by the use of post harvest laboratory tests. The use of serological tests developed during the last several years is making it possible to detect symptomless infections accurately. The development of monoclonal antibodies has helped to provide a degree of specificity and sensitivity that has not previously been possible (6). The full potential of detecting low bacterial populations with monoclonals has not yet been realized but ongoing research, by providing additional specific monoclonals, is expected to increase sensitivity and specificity.

The possibility of using cDNA probes as a sensitive and specific technique for detecting bacteria is also currently being investigated in the U.S. and Canada. Such a technique has been used to detect Escherichia coli in foods with a sensitivity level of 100 cells/g (10). The procedure involves isolating a segment of DNA unique to C. sepedonicum, cloning the DNA segment in another bacterial host, purifying and labelling the cloned DNA (usually with a radioactive label), and finally using it to probe the DNA fraction of a sample fixed to a nitrocellulose membrane. Whether this technique will provide the required degree of specificity still needs to be shown since some difficulty in obtaining adequate specificity has been encountered (N. Gudmestad, personal communication). It also remains to be seen whether sensitivity will be high enough to detect low levels of infection. However, the recent successful detection of spiroplasmas and mycoplasma-like organisms in plants and insects with DNA probes is encouraging (23).

Sensitive detection procedures are not only required to detect symptomless potato infections but are also a necessary research tool to resolve questions regarding the ecology of the ring rot pathogen. It was indicated previously that our knowledge of the biology of the bacterium was insufficient to determine whether eradication of the pathogen was even feasible. Detection of low levels of bacteria in soil and in alternate hosts has essentially been impossible until now. The establishment of sugarbeet as an alternate host for C. sepedonicum was only possible with the availability of specific monoclonal antibodies (N. Gudmestad, personal communication). Further investigation into the survival characteristics of this bacterium in the field is only just beginning but should provide important clues to assess the practicality and success of ring rot eradication. Although our appreciation of its survival capability has increased during the last several years, many questions still remain. We have no idea whether it can survive in animal manure, in ground water, or in association with insects, for example.

In addition to current research interests, advances in biotechnology may provide novel solutions to plant disease problems. Insertion of specific genes into plants is becoming a possibility. Perhaps a gene for resistance to bacterial ring rot can be found and inserted into the potato genome. Alternatively, a bacterium producing a toxin to *C. sepedonicum* can possibly be made for inoculation onto seed pieces. Such a scheme for protecting root cuttings against *Agrobacterium tumefaciens*, the crown gall pathogen, has already been successfully employed (14). Maybe one day seed pieces can be protected against ring rot infections in a similar manner.

CONCLUDING REMARKS

With the current state of our knowledge, disease eradication is still the best bet for ring rot control. Despite many gaps in our knowledge, positive recommendations can be made that are likely to bring success. Success can only be achieved, however, if there is a real commitment by potato growers. It is the potato growers, themselves who must implement the changes in potato production to prevent ring rot. Some of the recommendations will affect practices that have been followed for many years; others will have economic consequences. It is clear that, with current practices, the ring rot disease has not been eliminated and there is no reason to believe it will be if some action is not taken. Costly medication and changes in lifestyle are often necessary to cure or prevent diseases of man. So also positive action is required to solve plant disease problems. Bacterial ring rot can be controlled, but the price must be paid.

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CONTROL OF OTHER BACTERIAL DISEASES

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ABSTRACT

Recommended control measures for bacterial diseases of potato other than bacterial ring rot were reviewed. Most effective control has been obtained with an integrated approach that utilizes appropriate agronomic practices, production of disease tested nuclear stocks, disease resistance and chemical treatments to some extent.

Une revue des méthodes de contrôle des maladies bactériennes de la pomme de terre autres que la flétrissure est présentée. Le contrôle le plus efficace a été obtenu avec l'approche intégrée, qui utilise les pratiques agricoles appropriées, des stocks de base testés contre les maladies, la résistance aux maladies et dans une certaine mesure, les traitements chimiques.

INTRODUCTION

In the Canadian context there are four diseases of potato other than Bacterial Ring Rot Corynebacterium sepedonicum (Spieck & Kott.) Skapt. & Burkh. (BRR) caused by bacteria (10). These organisms and the common names of the diseases they incite are as follows: 1) Erwinia carotovora subsp. atroseptica (Van Hall) Dye, blackleg, 2) E. carotovora subsp. carotovora (Jones) Dye, soft rot, 3) Pseudomonas fluorescens Migula, pink eye and 4) Streptomyces scabies (Thaxter) Waksman & Henrici, common scab. A fifth organism, P. solanacearum E.F. Smith, which causes bacterial wilt has not been reported from potatoes in Canada, but is also of interest in that it causes considerable losses in offshore markets to which Canadian seed potatoes are exported.

The convenors of this symposium had requested a review of Canadian research on the subject of bacterial control. If published reports are used as indicators, Canadian research on control of bacteria other than BRR is not particularly plentiful. A literature search for the last ten years revealed five citations by Canadian authors. As well, the Inventory of Canadian Agricultural Research (ICAR) revealed just two people working with bacterial diseases other than BRR, Drs. S.H. De Boer and R.J. Copeman at Agriculture Canada and U.B.C., Vancouver, respectively. Two others, Dr. G.A. Nelson (60) and A. Frève, work with common scab and blackleg, respectively. While these findings may be indicative of an incomplete inventory, it would seem that research in Canada on the control of bacteria other than BRR is not extensive at present. Consequently, this paper will focus on recommended control measures, with the aim to stimulate discussion on the problems of control and the requirements for future research. The control of bacteria already relies on an integrated approach as will be seen from the methods that are utilized in minimizing disease.

SOFT ROT ERWINIAS/BLACKLEG

The erwinia bacteria, amongst the most destructive of organisms, are worldwide in distribution and cause losses in the field, transit and especially in storage . The distinguishing feature of the soft rot erwinias that separates them from other erwinias is the capacity to produce pectic enzymes that permit maceration of parenchymatous tissue (66). These diseases have been recognized for about 100 years and although progress has been made over the last 10-15 years, much remains to be elucidated.

There are three soft rot erwinias associated with potatoes, *E. carotovora* ssp. *carotovora* (Ecc) E.c. ssp. *atroseptica* (Eca) and *E. chrysthanthemi* (Echr), and their geographic/climatic distributions reflect the ranges of their hosts and temperature optimas (66). Eca and Ecc are rod-shaped, gram-negative bacteria with peritrichious flagella that are non spore forming and facultatively anerobic (27). Eca is restricted primarily to potatoes in the temperate regions of the world and until about twenty years ago was the only pathogen thought to be associated with stem infection (blackleg) in the field (65). This organism may cause disease in hotter climates when contaminated seed potatoes from temperate zones are planted, yet it is generally considered to be a poor soil survivor and tuber contamination disappears in one or two generations. Reports from Ireland (45), Scotland (24) and the U.S.A. (5,17) indicated that Eca levels declined to a very low level in soil following rotations. Ecc, on the other hand, has a worldwide distribution and can survive in many environments. Ecc is the predominant organism isolated from soil (5,69), surface water, irrigation water and aerosols (16,23,26,31,56,62,70,71). Enrichment techniques and serological strain typing methods have been used to determine the source of stem and progeny tuber populations of *E. carotovora*. Ecc was isolated more frequently from seed, soil, stems and progeny tubers in Wisconsin (52). These results indicate that the potential for reinfestation of seed stocks is greater than was thought initially. The third erwinia, Echr attacks a broad range of tropical and sub-tropical crops and had been considered to have a tropical distribution, but has recently been isolated in some cool temperate countries (65). Although this organism would be considered a rarity in the potato-growing areas of the northern hemisphere (32), it nevertheless poses a potential problem as the cultivation of potatoes spreads increasingly to the subtropics.

The symptoms caused by the erwinias vary depending on the environment, pathogen, cultivar and plant part affected. Symptom expression can occur any time between emergence and harvest but Ecc, Eca and Echr will all produce symptoms of blackleg under conditions that favour disease development. Soil, air temperature, and moisture levels influence blackleg expression (26). Classic blackleg symptoms are promoted by cool moist conditions just after planting, followed by a warm, moist post-emergence environment (64,66). Warm soil temperatures at planting may promote rapid decay of the seed piece which leads to non-emergence. Rapid decay of the stems is caused by high moisture; dry weather, on the other hand, may limit the decay and result in selfelimination (26). This close interaction between disease development and environmental conditions explains why seed potatoes from one lot planted at different times or in different locations may express quite different levels of disease (26).

A large proportion of tubers from a seed lot may be contaminated on the surface, in lenticels or in vascular bundles (15,53). The presence of bacteria within the vascular system is one reason why bactericides have not been effective. The potential then for soft rot exists, especially if tubers are damaged by mechanical harvesters (32), graders, or during storage and transit. Water films that remain on tubers following washing or chemical treatments, from condensation or from tubers rotting from other diseases reduce O_2 levels and favour soft rot development (6). The inoculum threshold for soft rot is much lower on wet tubers (66). Prompt drying and adequate ventilation of tubers are effective means of controlling soft rots. A review of the ecology of the soft rot erwinias was published in 1980 (66).

Some idea of the extent of the problem caused by erwinias can be obtained from a 1984 report that revealed the incidence of potato disorders recorded at the New York market over a nine-year period. Bacterial soft rot was the most common disorder with 5,208 reports in 13,757 shipments. Three hundred and twenty-seven Canadian shipments were reported and bacterial soft rot was present in 42% of the loads (8). Furthermore, the significance of the disease was emphasized by the evidence presented at the 1st International Conference on Potato Blackleg held at Edinburgh, Scotland in 1984. At that time, 57 participants, including three Canadians, from 13 countries met to discuss the disease, its causes, epidemiology, effects on seed certification programs and seed exports as well as control measures. The proceedings were published in 1985 and provide a useful starting point in appreciating the many aspects of the disease (25).

Effective control of blackleg and soft rot has been inconsistent. Control of these diseases is more complex than with simple wound pathogens since the bacteria are ubiquitous and there are 3 phases of the disease cycle that require control. Firstly, a large proportion of the tubers carry sufficient inoculum to initiate disease; secondly, the bacteria from seed or other sources can colonize underground parts of the plants and can infest daughter tubers; and thirdly, rots can be initiated in storage or transit (74).

The use of appropriate agronomic practices, disease tested nuclear stocks combined with seed certification systems, biological control and resistance breeding actually constitute an integrated approach to minimize loss. Each of these categories will be dealt with separately below. Essentially, the strategy is to decrease the levels of inoculum and minimize the opportunity for disease spread and damage to the growing and harvested crop.

1. Agronomic Practices

One outcome of the 1st International Blackleg Conference was an outline of agronomic advice to potato growers for minimizing blackleg. While all the advice is not appropriate for the situation in Canada, the 14 point guideline for control is reproduced below.

Outline of advice to potato growers to minimize blackleg disease from the Report of the 1st International Conference on Potato Blackleg Disease (25).

1. "The basis of any scheme to minimize blackleg is production of erwinia-free nucleus stocks obtained by stem cutting or tissue culture methods (micro propagation). Use of these stocks coupled with limited (restricted) generation schemes to reduce contamination can have major beneficial impacts on blackleg control.

2. Plant only healthy seed. Obviously damaged or diseased tubers should not be used.

3. Plant as soon as soil temperatures and other conditions are favourable; factors such as soil temperature and moisture have considerable effects on disease expression. When possible use presprouted (chitted) seed to ensure rapid establishment of plants. However, it is notable that under certain conditions, pre-sprouting can increase blackleg expression.

4. Use fertilizers at recommended rates. Lack of nitrogen increases blackleg expression whereas excessive nitrogen can result in increases in tuber soft rot.

5. In cool wet climates, harvest as early and as carefully as possible in dry conditions; in warm dry climates be sure that adequate soil moisture is available to minimize tuber damage. Ensure that tubers are mature to avoid excessive skinning and avoid tuber damage throughout all stages of harvesting and storage.

6. In areas of the world where wet harvesting conditions are common, keep potato storage conditions dry, and dry tubers as quickly as possible after harvest. The use of windrowing or other harvest methods to accomplish this should be considered. Forced draught ventilation can be very useful for this purpose. In areas of the world where dry conditions prevail at harvest, however, humidification of ventilation air is required to assist wound healing and to prevent weight loss.

7. Destroy haulm with a quick-acting desiccant if green foliage or stems remain at harvest time; do not pulverize until haulm is dead especially in wet climates where *Erwinia* aerosols generated by haulm pulverization can survive for relatively long periods.

8. Clean and disinfect stores, boxes and farm machinery regularly. Grading equipment should receive special attention, especially if stocks contain soft-rotted tubers. Different grades and stocks of tubers should be stored separately.

last 10 years in New Brunswick, the number of rejections for blackleg has dropped due to better sanitation practices on farms and the introduction of a flush through seed system (E.M. Smith, Agriculture Canada, Fredericton, pers. comm.). The production of nuclear stocks from disease tested stem cuttings or in vitro plantlets to control virus disease certainly has had the added advantage of reducing blackleg incidence. Knutson (36) concluded that stem cutting effectively eliminated Ecc and Eca from infected seed stocks and seed stocks so derived remained free of visible blackleg for 2-3 seasons. Rates of recontamination were variable and the contributing factors were not always apparent. Stem cut seed stocks had greater stand, were more uniform and exhibited superior yield and quality than non stem cut stocks (15). De Boer reported that the introduction of a stem cutting program in the Pemberton Valley in B.C. in 1978 had reduced the incidence of blackleg; however, Ecc re-infestation was high. While yield losses due to blackleg may have been reduced, the latent infestation of seed tubers for export to warm countries may present a problem (E.M. Smith, pers. comm.).

Although most commercial stocks of seed potatoes are contaminated to some extent by soft rot bacteria, the expression of disease does not necessarily result. Conversely, recent developments in the etiology and epidemiology of blackleg indicate that irrespective of the presence or absence of blackleg in the parent crop, seed contamination may occur. The sources of the contamination may be: 1) the mother tuber which rots and releases bacteria that infest progeny tubers, 2) bacteria from aerosols or from insects which are deposited on leaves and that eventually wash down into the soil and onto tubers, 3) bacteria spread via irrigation water, and 4) grading machinery that can spread bacteria very effectively (65). These factors explain the problem encountered with disease-free stocks that gradually become contaminated.

Since a diseased plant is not primarily responsible for transferring disease from one generation to another, roguing and inspection cannot guarantee complete control (65). Nevertheless, the presence of infected plants in seed crops is undesirable since they provide another source of inoculum. At the blackleg conference in 1984, there was some debate about the merits of setting disease tolerances. No consensus could be reached; some viewed tolerances as supplying useless information since they gave no indication of the level of the infection after inspection. On the other hand, it was felt that tolerances at least encouraged the removal of inoculum and, furthermore, a country that does not rogue for blackleg would be at a competitive disadvantage to those countries that do so (65). Practical methods to assess seed contamination are being developed (51,65) with the aim of providing a measure of tuber contamination which can be related to the incidence of disease in the field. This may be one avenue to consider when exporting seed, especially to those countries that have had considerable blackleg problems.

3. Biological Control with Rhizosphere Bacteria Antagonistic to Soft Rot *Erwinias*

The approach of using specific micro-organisms to control plant diseases is still in the developmental stages when compared to the indirect methods of influencing micro-organism populations by crop rotations and green manuring (74). The idea is to identify and select bacteria from potatoes that are antagonistic to *Erwinia* sp.

Fluorescent pseudomonads have been identified as candidates since they colonize the rhizoplane, rhizosphere and plant parts in high numbers (1,34,35,48). Coyler & Mount (12) and Kloepper (33) showed that soft rot pockets could be reduced in daughter tubers by the application of pseudomonads. The degree of soft rot was also lessened with a mixture of *Bacillus* and *Pseudomonas* spp. (75). Recently, a procedure to screen fluorescent pseudomonads from potatoes for soft rot suppression was developed (83). The method is based on antagonism *in vivo* and the suppression of pre-emergence seed piece decay.

There are many factors to consider when evaluating the potential of a bio-control agent. For instance, the period of host susceptibility to infection by *Erwinia* is long lasting so an effective biocontrol agent must be present at all stages of susceptibility. The competitive ability of the antagonists would have to be determined since conceivably it would be difficult to displace other established soil inhabitants. It may be advantageous to develop antagonistic micro-organisms for particular ecological niches. When one considers the diverse potato-growing regions, it is apparent that mixtures of adapted micro- organisms might stand the greatest chance of survival (65). Finally, for a biological control agent to be adopted, it must be competitive with other means of control both in cost and effectiveness and be applicable to farming practices. Considerable research will be necessary to bring the concept from experiment to application.

4. Control of *Erwinias* by Breeding for Resistance

There are a number of general comments that must precede any account of resistance breeding. For a breeding program to conduct crossing for resistance to a particular disease, several pre-requisites are necessary. The character must be heritable, sources of variation must exist within the germplasm collections and it must be possible to differentiate between resistant and susceptible individuals. In addition to the disease resistance, yield, horticultural attributes and quality must be assured. Potatoes are subject to many diseases and whether the time-consuming and costly process of breeding for a disease resistance takes place will depend on the extent of the disease problem, whether the disease can be controlled effectively by other means, and the likelihood of achieving success.

Erwinias are not given a high priority and many programs do not actively breed for resistance. Instead, as in the case with the

9. Maintain a high standard of hygiene on the farm. Do not accumulate waste potato piles. Control weeds - their roots can harbour blackleg and soft rot bacteria.
10. When using irrigation for high quality seed stocks, consideration should be given to treating surface water (using commercially available filters or ultraviolet treatment) to eliminate *Erwinia* bacteria. However, such treatments may be prohibitively expensive for use with lower quality seed and ware crops. Deep well waters appear to be relatively free from *Erwinia* and may be used without treatment. The amount of water used should be carefully regulated to avoid drought or waterlogging of the soil both of which may stress plants and increase losses due to *Erwinia* infection.

11. Roguing of seed crops to achieve seed certification standards is necessary where tolerances are operated. Roguing of ware potato crops is not economically justifiable.

12. Chemical treatment of whole seed tubers to control fungal rots should be considered by individual growers on the basis of their experience. Cut seed should always be treated with a fungicide to control fungus infections which can increase blackleg expression in the subsequent crop.

13. When compatible with local farming practices, seed growers who save their own seed for replanting and ware growers who do not intend to replace all of their stocks each year with classified stocks should consider maintaining a small nursery plot for production of their own seed as an alternative to saving seed sized tubers from their main crop. This plot should be carefully examined and all diseased plants rogued throughout the season, and should, when necessary, possible or practical, be certified officially. Cultivation machinery used in the rest of the crop should not be used in the nursery plot without prior disinfection. The nursery plot tubers should be stored in clean containers separate from the rest of the crop.

14. Plant whole (uncut) seed tubers whenever possible. When planting cut seed be sure the cut surfaces are well healed or that they are planted into soil with the proper conditions for suberization and healing to occur. As mentioned earlier, cut seed should always be treated with a fungicide. When cutting seed, clean and disinfect mechanical cutting machines as often as possible and certainly between different seed lots."

2. Seed Certification/Disease Tested Nuclear Stocks

In Canada, blackleg/soft rot are proscribed diseases in the Seed Certification Act. To obtain EIII status, seed must pass three field inspections and have not more than 0.1% blackleg or a combined total with wilts and viruses of 0.25%. In Foundation and Certified seed categories, 0.25% and 2.0% are permitted, respectively. There is zero tolerance for soft rot in all classes of seed. Within the

Fredericton program, extreme susceptibility is identified and eliminated. Andrew Frève of Agriculture Canada, La Pocatiere co-operates with the Fredericton program by screening approximately 10 advanced lines per year. The tubers are inoculated and emergence, vigour and yield are compared with the resistant and susceptible checks by multivariate analysis.

There is evidence to indicate that genetic differences in susceptibility to blackleg (28) and soft rot exist (9,11,67,78). Separate breeding schemes are required for blackleg and soft rot since correlation between resistance to the two is not high (81). As yet no truly resistant or immune cultivar has been identified. Dobias (18) reported differences in combining ability of parental cultivars with the same level of soft rot resistance since there were differences in the mean resistance of their progenies. He also found that progenies of RxR and RxS exhibited higher levels of resistance than SxS crosses.

The drawback to screening programs has been the lack of reliable methods that effectively differentiate between the reactions of early generations. A number of researchers are addressing the problem of accurate screening methods (4,30,39,40,41,42,46,47,61,80). The advances in cell and protoplast culture have led to experiments designed to identify resistance in regenerants. The protocol for screening calli derived from protoplasts has yet to be ascertained (74). As with any screening method, resistant individuals that are identified must ultimately be evaluated in the field under standard growing practices. The reported synergistic effects of Verticillium dahliae (37,65,84) and Fusarium sambucinum (14) may confound field assessments of resistance.

COMMON SCAB

Common scab attacks stems, stolons, roots and most significantly young, growing tubers. Penetration takes place through lenticels and stomata prior to periderm development. Wounds and insect damage may also serve as infection sites (29). Infection is favoured in dry, light-textured soils as well as in soils with high organic content (49).

Common scab lesions on tubers may range from superficial russets to deep pits and affect the grade of seed stocks (10% light and 5% moderate scab is tolerated) and the marketable yield of table stocks. Although superficial lesions can be tolerated by the processing industry, deep pitted lesions increase peeling losses and reduce the quality of the finished product (49). Tubers with severe lesions are more subject to dehydration and invasion by secondary organisms in storage.

Streptomyces scabies, an actinomycete, is the primary causal agent and occurs in most soils where potatoes have been grown (29). A study of scab isolates from the North Eastern US and Canada indicated that at least 2 species of Streptomyces are responsible for damage, one of which was acid tolerant (50). A complex of species was implicated in a form of scab occurring in acid soils (54). Although Streptomyces spp possess a filamentous morphology, they are classed as bacteria since they are akaryotic and have bacteria-like biochemical characteristics.

An integrated approach to scab control is recommended to minimize disease. Hooker (29), Osborn (63) and Loria (49) have summarized the methods frequently used, which are as follows:

1. Avoid planting scabby tubers to prevent the introduction of inoculum to uninfested soil and to reduce the buildup of inoculum levels. Streptomyces spp are saprophytes and will survive in organic debris in the absence of a host for many years. Consequently, the addition of animal manure favours saprophytic survival and should be avoided where scab is a problem.

2. Increasing the length of time between potato crops and selecting rotation crops other than beets, fleshy rooted crucifers and carrots will reduce but not eliminate soil populations. Rotation is effective for controlling acid scab.

3. High soil moisture levels have been linked to scab control (73) and the possibility of using irrigation as a means of control was suggested (2,38,43). For adequate control when soil is dry, irrigation to field capacity must start at tuber initiation and continue for 4-6 weeks depending on the cultivar and climate. Theories to explain the effects of irrigation were summarized (2) as: 1) effects on tuber susceptibility, e.g. lenticel development, 2) direct effects on the pathogen by reduced temperatures or oxygen levels and 3) indirect effects on the pathogen through microbial antagonism or competition. Streptomyces spp grow well and will infect tubers in wet sterile conditions (H. Lawrence, Agriculture Canada; retired, Fredericton, pers. comm.); therefore, the influence of water on micro-organisms antagonistic to or having a competitive advantage over scab appears to be the most likely explanation. Irrigation is an intriguing control measure, but not practical in areas such as New Brunswick where irrigation is seldom practised.

4. Soil Management. With the exception of acid tolerant isolates, common scab is generally less severe as the pH drops below 5.2. As a result, it is suggested that soil be maintained at pH 5.0-5.2 with acid-producing fertilizers, e.g. ammonium sulfate, and with lime. The adjustment of pH in well-buffered soils may be impossible. Other shortcomings to control through pH adjustments are that as pH decreases so does nutrient availability and promising alternate crops such as peas have high pH needs.

5. Chemical control can take the form of seed piece treatments such as Mancozeb (complex of zinc and maneb containing 20% manganese and 2.5% zinc) or zineb [zinc ethylenebisdithiocarbamate (polymeric)] (49). Soil amendments with PCNB

[(6-methyl-1-oxo-1,3-dithiolo (4,5-b) quinoxaline pentachloronitrobenzene] have been effective (13,21,68) (PCNB is not registered for use on potatoes in Canada). A novel approach was the foliar application of growth regulators to control scab (57,58,59). Daminozide (N dimethylaminosuccinamic acid) and gibberellic acid (GA) reduced scab expression but less so than PCNB, and GA caused severe tuber distortions. Acid scab was controlled with systemic insecticides which led to the discovery of the possible role of springtails, mites and flea beetles in the development of acid scab (55). These authors also speculated that those arthropods may be involved in the etiology of all scab development.

6. Resistant cultivars. There is considerable variation in the reaction of potato cultivars to scab. However, when conditions are ideal for scab development, even cultivars with good degrees of resistance will become infected. Breeding programs all over the world screen material for resistance and Fredericton is no exception. For over 25 years, breeding selections at the 5th field generation stage have been exposed to scab in a disease plot maintained at the Fredericton Research Station of Agriculture Canada. Seedlings are rated for the extent of surface area covered, pustule type and are assigned resistance values in relation to standard check cultivars. The sources of resistance can be traced to parents such as Hindenburg, Richter's Jubel and USDA X96-56 that are not particularly well adapted to North American conditions. High levels of resistance have been identified in the germplasm collections and should broaden the base of resistance. Greenhouse tests have been developed as an alternative to field tests (3,7,19,20,44,82). Bjor & Roer's method has been adopted at Fredericton to permit screening of earlier generations and progeny testing. The use of micro-propagated plants may also be advantageous (79) and in vitro techniques using toxins produced by Streptomyces spp may also find application (Lawrence & Farrel, retired Agriculture Canada scientist and Postdoctoral Fellow, Fredericton, pers. comm.). Soma clonal variants with improved scab resistance have been reported from the susceptible cultivar, Désirée (22).

PINK EYE

The literature on pink eye is scarce. The disease is not considered a major problem, although differences in cultivar susceptibilities have been noted (E.M. Smith, pers. comm.). Infection may follow bruising and can cause seed tuber decay; there was also a report of the association of Verticillium wilt with pink eye (23). Control can be achieved by providing cool, dry storage conditions (29).

In closing, a few remarks about a serious disease of the tropics and sub-tropics, Pseudomonas solanacearum. The most practical control would be obtained through resistant cultivars (72,76,77). All current Canadian and most American and European cultivars are susceptible.

Sources of resistance in Solanum species such as S. phureja and S. stenotomum have been identified and some of these sources are present in the germplasm collection at Fredericton. The development of resistant cultivars for export would offer considerable advantage to Canadian seed exporters. Screening of selections would of necessity have to take place in co-operative trials in a country where the disease is endemic, since P. solanacearum has not been isolated from potatoes in Canada.

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POTATO LATE BLIGHT AND ITS CONTROL

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ABSTRACT

Potato late blight has been the major fungal disease of potatoes around the world for over 100 years. Research efforts have provided information about the pathogen, disease development, and control methods. These have greatly improved the opportunities for successful production in many locations. However, losses due to late blight still average more than 5% of production at a time when food shortages are causing death due to famine. In the past 20-30 years, successful research efforts have provided improved fungicides and application procedures, potato cultivar resistance, etc.. Future studies in the area of disease management or integration of disease control methods will further enable producers to avoid crop yield and quality losses due to late blight.

RESUME

Le mildiou de la pomme de terre est la plus importante mycose de cette culture dans le monde depuis plus de 100 ans. Les travaux de recherche ont fourni des renseignements sur l'agent pathogène, l'évolution de la maladie et les méthodes de lutte, et ont grandement amélioré les possibilités de production dans de nombreuses régions. Néanmoins, les pertes dues au mildiou restent supérieures en moyenne à 5 p. 100 de la production, et ce à une époque où les pénuries d'aliments causent encore des famines meurtrières. Depuis 20 ou 30 ans, les recherches ont permis de perfectionner les fongicides et les modes d'application, d'accroître la résistance des cultivars de pomme de terre, etc.. Les études futures sur la lutte contre les maladies ou sur les méthodes intégrées de lutte contre les maladies permettront aux producteurs d'éviter encore mieux les pertes de rendement et de qualité dues au mildiou.

INTRODUCTION

Native to Peru, the potato has had and continues to have a great deal of influence on the peoples of both the "developed" and the "underdeveloped" nations in the world. Introduced to Europe in the late 1500's and to the "New World" about 1620, the potato soon became a major food staple for the peasantry and an expensive delicacy for the nobility. Its introduction was particularly important for the peasants of Ireland where the potato became the main dish providing improved survival in an area under severe political, economic, social, and religious injustices (16). Potato cultivation became more widespread and significantly contributed to the decreases in famine during the 18th century.

Just as the potato became a major crop in Ireland both in terms of cultivated acreage and in regards to nutritional and economic "health", so did coffee in Ceylon and Brazil and wheat in North America. Unfortunately, as the acreages and dependence on these monocultures (the widespread cultivation of a single crop type) increased, so did the opportunities for disaster. From 1845 to 1847, the potato crop of Ireland was devastated by late blight. Similarily, major economic disasters occurred in 1870 in Ceylon and during the 1900's in Brazil and in North America due to epidemics (coffee rust, wheat stem rust, chestnut blight, "Dutch" elm disease, etc.) caused by other fungal pathogens of crops also under monoculture situations. With the potato late blight epidemic in Ireland, the results of the crop loss due to the disease included both economic failure and death because of famine. In addition, mass emigration occurred due to the unknown and unexplainable failure of the crop that for so many years had provided improved living conditions for the people of Ireland (16).

Since the Irish potato famine, many efforts have been made to understand and control the disease that caused so much damage. It is the successes and failures, particularly as related to the potato industry of Canada, that are described in this paper. In addition, current research activities and future opportunities will be discussed.

1870's TO 1970's

When late blight was devastating the potato crops of Ireland, people were not only starving but also perplexed. In 1845, no one knew the cause let alone the cure of their plight. The science of plants and their diseases was still in its infancy. Debates by chemists, philosophers, clergy, and medical men failed to successfully convince all others that "the" cause and cure had been uncovered. Finally, through the claims that the moon, fog, and/or soil were the causes, came the "Fungal" theory. This theory suggested that the moulds and mildews often seen on decaying plants and vegetables were not caused by the disease but instead caused the disease (22). The Rev. M.J. Berkley, a strong advocate of this theory, did much to advance its belief with his microscopic study of potato late blight. However, it was Speerschneider and deBary who finally proved experimentally that the fungus Phytophthora infestans (Mont.) deBary is the cause of the disease (1).

In those early years, trial and error was the general recommendation for late blight control although a lot of common sense and proven controls for medical diseases were often practiced. For example, fire was a recommended remedy and, in the majority of cases, seemed better or at least easier than "washing" or "flooding". About 1870, another method for control of late blight was discovered. This involved a disease that was a constant hazard to the grape growers. Vineyards were often damaged by a "fuzzy" fungal growth similar to that which caused late blight. However, in France, some common products (copper sulfate and hydrated lime) of the time were found to successfully control the grape mildew (16). This compound was soon commonly used to control potato late blight by sprinkling the mixture by hand onto the plant foliage. Thus began the use of chemicals for the control of potato late blight and other diseases of agricultural commodities.

During the last years of the 19th century and the early 1900's, researchers and growers alike learned more about how the disease was caused and the practical problems resulting from its occurrence in the field. For example, it was recognized that wet seasons often result in more disease than years with dry growing conditions (2). Furthermore, when the moist conditions continue during the harvest period, the stored crop will rot due to fuzzy white growth of the late blight organism in the potato tubers. These and other findings that have occurred in the past 100 years and that constitute the knowledge acquired during this time can be grouped into several categories - disease occurence, disease symptoms, the causal organism or pathogen, disease development and disease control.

Disease Occurrence:

Late blight is the most destructive disease of potatoes and is found in all potato production areas of the world. It is most damaging in eastern Canada, northeastern United States, northwestern Europe, and wherever large acreages are grown without fungicide usage for late blight control (except for hot, dry areas). These agricultural regions all suffer greater incidence and damage since potatoes are grown over large areas and the cool, moist weather conditions that normally occur favor both the growth of the crop and the pathogen.

The disease attacks the potato foliage and stems, killing the plant. As well, the tubers of the potato can become infected and then rot in the field, during storage, in transit, or at market. Late blight can also attack other species of Solanaceae such as tomato.

When weather conditions are favourable for disease development and control measures are not employed, the disease can completely destroy a field of potatoes within about two weeks. Crop yield losses vary in different regions depending on the climatic conditions, time of attack during the growing season, cultivar type grown, and control measures practiced. In addition, the tubers may be infected and postharvest rots add to the losses. In Prince Edward Island, crop losses of 20-100% in the field and at the end of the growing season have been recorded

(Table 1 - Platt, unpublished results).

Losses due to late blight can also occur at the market place even though a number of grading operations will have been made but which do not always eliminate all of the disease. For example, in the New York market, which is supplied by the production areas in the eastern U.S. and Canada, late blight has been found to cause 0.5% of the disorders (=10,000 t of potatoes lost annually) occurring in the table market (11).

Table 1. Potato Crop Losses Due to Late Blight on Prince Edward Island.

Year	Diseased Plants (%)	Diseased Tubers (%)
1986	92	4
1985	99	10
1984	100	22
1983	100	43
1982	100	26
1981	88	0.4
1980	100	12
1979	100	6

Note: Data from field trials not treated with disease control fungicides.

Disease Symptoms:

Potato foliage symptoms often first appear as water soaked, irregularly shaped, pale green spots. However, these lesions can vary depending on temperature, moisture, and light conditions as well as the host cultivar and the age of the leaf (2,12). In wet weather, the lesions can enlarge rapidly forming brown, necrotic areas which are often bordered by a pale green to yellow halo. A zone of white, fluffy fungal growth appears on the underside of the leaf at the edge of the expanding lesion. This mycelial and sporangial growth is clearly visible during or shortly after periods of dew or rain. The lesions will continue to spread across the leaf infecting the petiole and stem, eventually killing the entire plant. The rotting plant tissue has a very distinctive odor.

Potato tubers can also become infected, initially displaying irregular, purplish-black or brownish blotches with a somewhat shiny appearance on the tuber surface. Affected subsurface tissues are water soaked and reddish-brown in color. On the surface of the tuber, symptoms may eventually appear shrunken and dry. However, secondary organisms often follow the late blight infection causing a complete breakdown of the tuber tissue.

Causal Organism:

Late blight is caused by the fungal pathogen *Phytophthora infestans*. It is a phycomycete with hyaline, lemon-shaped sporangia that are borne on sporangiophores with characteristic swellings at the points where sporangia are formed. Sporangia germinate at temperatures between 1.5°C and 24°C with zoospores forming at temperatures up to 12°C -15°C and with sporangia developing germ tubes directly at temperatures greater than 15°C (1). Zoospores require free water to move but then eventually encyst and produce germ tubes. Germ tubes enter the plant via leaf stomata or directly through the cuticle by the formation of appressoria. Intercellular and intracellular penetration by the aseptate mycelium occurs once the organism enters the plant tissue.

For sexual reproduction, the organism forms oogonia and antheridia which produce oospores. Oospores germinate via germ tubes with terminal sporangia. Two mating types (A1 and A2) are required for sexual reproduction which enables the creation of new races of the pathogen. These mating types are only found to any extent in Mexico, so oospores are not commonly found in most potato production areas of the world.

Disease Development:

In most potato production areas, disease development begins with the potato tuber in which the pathogen overwinters. In tropical regions, where potatoes are cropped year-round, overwintering is not a problem for *P. infestans* as it survives by spreading from one crop to another. Elsewhere, the planting of infected tubers or the occurrence of infected volunteer plants provides the initial inoculum source for infection of the new crop. Spread by wind and water, the spores can attack both healthy and weakened plants. Infection is most successful under cool, wet weather conditions. Newly formed lesions become inoculum sources as the sporangia form on the undersides of infected leaves. Production is optimal at about 21°C and 100% humidity. Lower leaves are often heavily infected because of the high humidity in the lower portion of the crop canopy. Similarly, portions of a field protected from intense sunlight, wind or other drying conditions generally are more severely damaged. As the plant becomes heavily infected and the production of sporangia increases, normal tuber growth and development is stopped and yields are decreased. In addition, the opportunity for tuber infection increases. Spores washed by rain into the soil or onto exposed tubers cause tuber infections by entering through lenticels or wounds. These infected tubers can rot completely in the field or later in storage, at market, etc.. They also initiate disease problems in the following year's crop when infected tubers are planted or give rise to "volunteer" plants.

Disease Control:

Potato late blight can be successfully controlled by following a combination of crop sanitation and management recommendations, by utilizing the available potato cultivars with resistance to the disease, and by properly applying well-timed and efficacious fungicides.

Crop sanitation and management measures are necessary to avoid the primary or early season inoculum and to control the disease as it develops during the growing season. While some of these control measures were discovered by the early 1900's, others have only recently been recommended as farming became more mechanized and as research uncovered answers to new problems that modern crop production encountered (5). For example, planting healthy seed avoids the establishment of the disease in the field via the spread of the pathogen from infected seed tubers to the rest of the crop. Similarly, the destruction of "volunteer" plants and cull piles eliminates them as possible sources of the disease early in the season. This has been found to be particularly true on Prince Edward Island. Although highly dependent on the climatic conditions in the region, the first occurrence of late blight on Prince Edward Island is generally in early to mid-July, about 7-10 days after it has been reported in neighboring potato production areas. However, in 1983 unusually wet spring conditions resulted in an excess of unburied culls. This coincided with first late blight occurrence reports in late June to early July (Platt, unpublished).

Disease control also involves hilling operations as good soil coverage for the developing tubers is required to limit opportunities for tuber infections, particularly at the end of the growing season. In addition, the use of fungicides at the time of top desiccation can help to control late blight tuber rot (26). Harvest should also be delayed for about 2 weeks after top desiccation to prevent tuber infection by any late season inoculum.

Crop management measures for disease control should also be continued after harvest. By providing storage conditions which promote tuber wound healing after harvest followed by maintenance of proper temperature and humidity conditions for long term storage, damage due to late blight can be controlled.

In the past 30-40 years, utilizing the genetic resources within the potato to control late blight has been an important and active goal of research centers in all the major potato production areas of the world. New information about the host-plant/pathogen complex and new techniques for assessing disease responses has led to greater opportunities for disease control (20,27,31,32). In New Brunswick, potato breeding efforts have resulted in the development and release of new potato lines, such as F74123 and F73008, with resistance to late blight (D.A. Young, unpublished data). For potato late blight, as with most host-plant/pathogen complexes, two types of resistance are recognized: 1) specific or vertical resistance and 2) general or horizontal. Vertical resistance within a potato cultivar refers to the capacity within that particular host to resist attack by a specific race of the pathogen. However, that same cultivar can also be susceptible to another race of the pathogen that may currently exist or that could be formed in the future by the pathogen. For example, Kennebec, Cherokee, Fundy, and Onaway are resistant to single races of P. infestans. However, since P. infestans is a highly variable pathogen with the capacity to produce new races, it can often overcome this type of resistance.

Horizontal resistance refers to a cultivar's ability to withstand attack by the pathogen without major damage to its growth and yield capacity. This type of resistance is only partial but is effective against a large number of races. Thus, it is more difficult for the pathogen to overcome. Sebago is a potato cultivar which has horizontal resistance.

Unfortunately, varietal resistance to late blight in most cases cannot be solely relied upon for disease control. This is in part because resistance to foliar attack does not ensure resistance to tuber blight. Thus, under ideal climatic conditions for disease development, blight could spread rapidly and cause major tuber damage. For this reason, use of fungicides for late blight control are generally recommended regardless of the cultivar's disease response. Furthermore, fungicide usage is useful in limiting the possibility of the pathogen developing new races where cultivars with vertical resistance are grown and to prevent the crop from being attacked by a race to which the crop is not resistant.

The proper application of efficacious, well-timed fungicides has become a vital practice in all major potato production areas. Since the discovery and early use of fungicides such as Bordeaux mixture and the arsenates in the late 1800's, fungicide research and development has been an ongoing effort, both from the standpoint of creating better types and also to increase our understanding of the disease and its control. However, it has been only in the past 30-40 years that new chemistry has been discovered and introduced for commercial application. In fact, many growers were still utilizing Bordeaux mixture and other inorganics such as the mercurials, which were developed after the Second World War, until the early 1960's. More recent discoveries include the organics, such as the carbamates, dithiocarbamates, etc.. Some of these have completely replaced the traditional fungicides because of the improvements in disease control efficacy and in the safety they offer. In general, most of these fungicides provided reasonable protection. However, this was dependent on the weather as it affected rate of disease spread, and on the proper application of the fungicides.

In the last decade, the potato industry has had access to new types of fungicides which do more than just protect the crop from the pathogen. The acylalanines have systemic activity which means they enter and are distributed within the plant. Previously, fungicides for late blight control were not able to enter and move within the plant. Instead, disease control involved the fungicide providing a "protective coating" on the plant that prevented the pathogen from attacking. Unfortunately, these protectants can be removed by rain and sun. In addition, protectants have to be constantly reapplied to protect the new growth of the plants. With the introduction of systemic fungicides, late blight can be prevented as well as being stopped. Systemic fungicides that move within plants can stop the pathogen after it has already infected the plant. That is, the disease can be eradicated.

Furthermore, systemic fungicides moving within the plant can be transported to the new plant growth and provide disease control. Unfortunately, systemics by their pathogen-specific nature suffer from the pathogen's capacity to produce races that are not controlled by the fungicide.

Currently available fungicides will generally provide acceptable to excellent control of potato late blight under most conditions. However, successful control depends on much more than just fungicide efficacy. Proper application practices must be followed to ensure that the fungicides will be in the correct place at the right time and in the necessary amounts to control the disease. For example, the spray must be applied so that fungicide reaches the bottom leaves which are often attacked first by the pathogen. It has been these considerations, as well as problems relating to host resistance and cultural methods for disease control, that have led to many of the current scientific investigations of the pathogen, disease development, and disease control.

THE PRESENT

Just as the Irish faced new problems 100 years ago when their lifestyles and cropping practices changed, during the 1970's and 1980's new solutions have been introduced to meet the current demands for potatoes and the control of late blight. Certainly, with the starvation on all continents, a measured world food deficit of 37 million tons of food in 1975, and a projected deficit of 120-145 million tons for 1990 when the population will have doubled, the need for improvements in food production systems cannot be ignored (23). For potatoes, a major food staple for much of the world, the statistics are just as alarming (Table 2). Up to 1960, potato production losses (in the U.S.A. alone) were about 20%, of which late blight resulted in a $20 million loss. In 1975, there was about $700 million worth of potatoes lost. Of course, additional financial losses are always borne by the farmers in terms of cost of production and these are increasing each year (Table 3). In 10 to 15 years, the use of pesticides including fungicides approximately doubled while the costs rose to a level of ten times what they were in the 1950's in the U.S.A..

Table 2. Potato Production Figures.*

1960 - U.S.A. potato production losses due to late blight	$20 million
1975 - U.S.A. potato production losses due to late blight	$702 million
1976 - World potato production losses due to disease 89 million tons	$3.4 billion

*Extracted from D. Pimental, Editor (23).

Table 3. Pesticide Costs and Usage.*

	Costs	
	U.S.A.	World
Fungicides - 1974	$116**	$961
All Pesticides - 1951	194	
- 1961	308	
- 1971	1,000	
- 1981	1,900	

	Usage in U.S.A.	
	Amount (kg)	Hectares Treated
Fungicides - 1966	15**	2
- 1976	19	4
All Pesticides - 1966	147	60
- 1976	292	97

*Extracted from D. Pimental, Editor (23).
**All values in millions.

In Canada, similar occurrences jeopardize the potato industry and this can also impact on those countries to which Canada exports potatoes (Table 4). With the major potato production areas in Canada situated along the eastern seaboard, costs of production are already high due to distances from markets. In 1984, costs were approximately $1840/ha with late blight control costs at 8-12% of the total (Statistics Canada, 1984 Annual Reports). When weather conditions favour late blight, crop losses as well as financial losses on purchased spray materials are incurred by the growers. Thus, the need exists for research into ever better, efficacious and economical, ways of dealing with this disease.

Table 4. Potato Production in Major Production Areas in Canada.*

1984	Acreage (ha)	Mean Yield (t/ha)	Total Production (tonnes)	Table Exports (tonnes)	Seed Exports (tonnes)
P.E.I.	28,800	30	858,600	96,937	68,751
N.B.	21,600	22	473,850	66,564	43,463
N.S.	1,640	24	-	28	-
Que.	18,800	22	406,665	11,856	8
Canada	115,480	24	2,728,215	200,105	122,546

*Extracted from Statistics Canada, 1984 Annual Report.

Current research is involved with a broad range of aspects of the disease and its control. This includes studies on cultural and environmental influences, on biochemical activities of the host-parasite interaction, on the manipulation of genetic resources in combination with fungicide application timings, etc.. Throughout the past 30-40 years, continued study of new fungicides for late blight control occurred with many Canadian researchers contributing substantially (7,8,26,34). These efforts led to improvements in the "protectant types" of fungicides used and to the recent introduction of the new systemic-type fungicides.

Table 5. Potato Late Blight Incidence with Use of Systemic Fungicides for Disease Eradication.*

Spray Treatment	Percent Foliar Disease (by day/month)					
1981	10/8	18/8	24/8	31/8	8/9	11/9
Metalaxyl	8	56	74	79	84	88
Untreated	22	77	88	97	100	100
1983	11/8	15/8	19/8	25/8	2/9	9/9
Metalaxyl	11	21	46	76	90	94
Untreated	17	30	54	81	94	96

*Extracted from H.W. Platt (28).

Furthermore, when the pathogen was found to have developed resistance to the systemic acylalanine fungicides in Ireland (15) and Holland (13), research in Canada contributed to an improved understanding of the situation and to a maintained access to this important means of control (5,6,28,29). For example, use of the "systemic" acylalanine fungicides alone for disease control did not eradicate late blight (Table 5). In Canada, potato producers currently have access to both the traditional protectant fungicides as well as the new systemic, acylalanine type in a combined form. This combination product, which combines the disease prevention capacity of the protectant fungicide with the disease eradication capacity of the systemic type, has been found to provide good control of late blight (Table 6). Similar results have been found elsewhere with other systemic-control fungicide mixtures (30).

Table 6. Potato Late Blight Incidence with Use of Protectant (Mancozeb) and Systemic (Metalaxyl) Fungicide Sprays.*

Spray Treatment	Percent Foliar Disease (by day/month)						
	27/8	31/8	4/9	7/9	10/9	17/9	20/9
Mancozeb	0.4	2.1	3.3	4.9	6.6	8.1	9.1
Mancozeb + Metalaxyl	0.1	1.0	1.3	1.8	2.4	2.5	2.5
Untreated Check	18.3	42.5	68.8	80.0	88.8	95.8	99.5

*Extracted from H.W. Platt (29).

Another area of research that is currently providing improved methods for late blight conrol involves disease forecasting. This research is not entirely new but has required many years of study in order to become commercially available and useful. Early studies involved work on the effects of climate and ecoclimate on the epidemiology of P. infestans, such as those by Hirst and Stedman (17), Callbeck (9), and others. In addition, research on assessing crop loss due to disease (19) and on use of computer generated crop models (4) has enabled the development of ever more accurate disease forecasting systems. Such a system is now available to potato farmers throughout the major potato producing provinces of Maritime Canada and is enabling them to select the optimal late blight fungicide spray times (3,18). A new system, Daycast, is providing growers with opportunities to eliminate unnecessary sprays and save money but maintain adequate disease control (see Holley, these proceedings).

In addition to these studies on fungicide efficacy and application timing, research into spray volumes and sprayer types has recently been initiated (10,24,25) (see also Kiley and Wiesner, these proceedings). While damage to other crops rarely occurs when fungicide sprays drift to non-target crops, spray drift is of concern. Improper fungicide application can leave portions of the crop unprotected, resulting in disease development and, hence, financial losses in terms of yield reductions and the loss of the costly chemicals. The recent introduction of controlled droplet sprayers has provided several benefits in regards to pest control and costs of pesticide usage, but research has demonstrated some weaknesses with the use of these sprayers as compared to conventional types for application of late blight control fungicides (25). On Prince Edward Island, research demonstrated increased late blight when a controlled droplet sprayer was compared to a conventional sprayer (Table 7).

Table 7. Potato Late Blight Incidence When a Controlled Droplet (CDA) and a Conventional Sprayer (CON) Were Used to Apply Fungicides.*

Sprayer Type	Percent Foliar Damage	
	1981	1982
CDA	73	76
CON	35	38

*Extracted from H.W. Platt and J.A.Ivany (25).

These are but a few of the research efforts that are currently being conducted. While failures have occurred, certain successes are evident by being in practice at the commercial level. However, not all of the problems are solved and, in some cases, research efforts and technological changes have uncovered new ones that must be worked on in the near future.

THE FUTURE

By its very aggressive and variable nature, P. infestans will continue to be one of the most difficult potato disease-causing pathogens to fully control. Its capacity to attack healthy plants, develop new races to new genes for resistance within the potato, and create new fungicide-resistant strains forces research to take a very broad investigative approach. Studies on all of the areas previously mentioned will have to be diligently continued. However, a new and necessary emphasis is currently emerging which should greatly improve the potential of attaining the disease control goals of research in the next number of years. This emphasis involves all of the various aspects of "disease management".

In the past, researches on certain disease control approaches were conducted in isolation of others. For example, development of new fungicides has not always been coordinated with the development of new disease resistant potato cultivars. However, it is becoming more generally recognized that future successes in late blight control research will involve an integrated approach. This emphasis will be necessary for both the research to be conducted in the traditional areas of investigation and also for studies in those new areas that have yet to be initiated.

In the traditional areas of late blight control research, such as breeding for disease resistance and fungicide development, opportunities for gains are good (23). With the continued exploitation of new germplasm with genes for resistance, new potato cultivars with previously unused genes for resistance can be used commercially (14,21, 33). Also, new cultivars will be developed with greater tolerance or field resistance to the disease. When these cultivars are used in combination with the proper use of fungicides, they should provide for a more stable overall means of control or disease management. Also, it should extent the usage period for both the cultivar and fungicide since the pathogen would be less able to quickly develop new races or strains against both. The recent successful introduction of protectant-systemic combination fungicides is indicative of the future potential of research in this area of late blight control. However, again, the greatest gains will probably result from integrated approaches. For example, use of disease forecasting systems with the new fungicides should not only save growers time and money but also prevent over-exposure of the pathogen to the new compounds and limit the development of fungicide resistant strains.

In terms of disease control, several aspects have yet to be researched (23). Not only can improvements be developed in the machinery (ground, aerial, and through irrigation) used for applying chemicals but also with respect to the interaction of the plant and fungicide. New research is just now demonstrating potential improvements with different sprayer styles and droplet size and electric charges. Fungicide tenacity, spreadability, and reaction on different leaf surfaces have yet to be fully studied.

Disease management in the future will also come from the continued research at the cellular level of the biochemical interactions between the fungus and the potato plant. Use of the natural defense system of the potato in combination with other disease control methods such as chemicals or breeding for disease resistance could, in the future, reduce costs or usage of fungicides. Much of the work to be conducted involves the plant and the pathogen but future research on manipulation of the environment may also yield useful tools for disease control. In addition, work on the effects of physiological "health" of the plant as affected by nutritional status and nutrient availability has yet to be fully explored in terms of disease control.

In conclusion, research efforts are required in a large number of areas to provide better control of late blight. However, successful disease control will demand disease management approaches. This will involve more integration of the various methods currently in practice or being researched into useful packages. The challenge is to provide the potato industry with cost-effective, efficacious means to prevent loss of crop yield and quality from the time it is planted until it is utilized as seed or a foodstuff.

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DAYCAST: A late blight forecasting program designed for Canada's Atlantic provinces - Successes and Failures

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ABSTRACT:

Spray recommendations generated by DAYCAST, a late blight forecast designed for use in Atlantic provinces, were tested in replicated field plots over three seasons. Analysis of apparent infection rates showed that the program provided adequate disease control on very susceptible cultivars in seasons with rapid disease progression. Further analysis, however, suggested that the program tended to recommend spray applications when they were not needed. This trend was evident on all cultivars in seasons with slower epidemic development but was most apparent on cultivars with greater levels of disease resistance. To be made cost effective, DAYCAST must be modified so that it more accurately identifies periods of low risk. Also, it must provide recommendations appropriate for cultivars with different levels of disease resistance.

RESUME:

Des recommendations de pulvérisations générées par DAYCAST, un programme de prévision du mildiou de la pomme de terre pour les provinces de l'Atlantique, furent mises à l'essais durant trois années dans des parcelles répétées. L'analyse des taux d'infection apparente démontra que le programme fournissait un contrôle satisfaisant de la maladie pour les cultivars très sensibles durant les saisons où la maladie se développait rapidement. Une analyse plus détaillée, cependant, suggéra que le programme recommandait des applications surperflues. Cette tendance etait évidente avec toutes les cultivars durant les saisons de dévelopment lent de la maladie, mais était plus apparente avec les cultivars plus résistants à la maladie. Pour devenir rentable, DAYCAST doit être modifié afin de prédire plus précisement les périodes de risque réduit. Aussi, il doit fournir des recommendations appropriées aux cultivars de différentes tolérances à la maladie.

INTRODUCTION:

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, spread so rapidly in Europe in the mid 1840's that the entire potato harvest was destroyed (1, 11, 28). The resulting famine, later called the Great Irish Potato Famine, not only killed hundreds of thousands of peasants but also was responsible for the mass immigration of Irish settlers into the Maritime provinces of eastern Canada (28).

Given cool wet conditions, *P. infestans* can defoliate the canopy of a susceptible potato cultivar in less than 14 days (1, 3, 4, 5, 11, 28). When blight occurs early and is severe, harvest weights can be reduced substantially (1, 5, 11, 19, 23, 28). Sporangia from infected vines can wash into the soil to infect tubers underground. Also, they can infect tubers at harvest as they are removed from the ground (1, 5, 11, 23, 28). Blight infected tubers generally are colonized by soft-rotting bacteria. This soft rot then can spread into healthy adjacent tuber tissues. When too many blight infected tubers are put into storage, extensive breakdown can cause serious economic losses (1, 11, 28).

Understandably, late blight is still considered a potential threat to potato production (1, 3, 5, 23). Rapid development of late blight, however, occurs only sporadically in the Maritimes (7, 8, 13 to 17). Often, epidemic development is slow and, in some seasons there is little evidence of late blight in commercial fields. Many growers, however, apply fungicides every 7 to 10 days as insurance against blight regardless of the conditions. Application of unnecessary sprays is not cost effective and adds pollutants to the environment needlessly. On the other hand, growers occasionally apply fungicides too infrequently and, if conditions favor rapid epidemic development, poor disease control not only creates problems for the careless grower but for those adjacent as well. Therefore, attempts have been made to develop disease forecasts to encourage growers to apply sprays when they are needed for cost effective control (2, 7, 8, 13 to 17, 20 to 25, 26, 27, 29 to 35).

BASIC ASSUMPTIONS FOR LATE BLIGHT FORECASTS:

Disease forecasts have been developed for only a few pathosystems to date (5, 23, 24). The potato late blight pathosystem was one of the first used to develop forecasting models because the disease was serious and conditions which generated rapid disease spread appeared to be specific and well defined (1, 2, 5, 7, 8, 11, 13, 20 to 24, 26 to 29, 31 to 35). Earlier research showed that at least 10 hours of relative humidity above 90% (2, 7, 20 to 23, 26, 27, 29 to 35) or more than 5 mm of rainfall (13 to 17, 20 to 23, 26, 27) were required in a 24 hour period for infection, provided that the daily maximum temperature remained below 30°C and the minimum above 7°C (20, 22). Conditions were thought to favor more rapid epidemic development as periods of high relative humidity increased, as amounts of rainfall increased and as mean daily temperatures increased.

In North America, arbitrary severity values are used in all forecasting models to reflect the previously described assumptions. In all models, severity values are totalled for 7 days prior to a given forecast date. Totals are used to determine how frequently sprays should be applied (2, 7, 8, 20, 21, 22, 26, 27).

DAYCAST: MODEL DESIGN

The DAYCAST model calculates severity values using a method which is similar to other forecasts (7, 8) (Tables 1,2,3). Unlike other models, however, DAYCAST assumes that inoculum density also affects disease progress.

Table 1. Daily severity values determined from hours of relative humidity (RH) above 90% and average temperature in degrees celsius (C).

Average temperature (C)	Hours of RH above 90%									
	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	37-39
7.1 - 11.6	0	0	1	2	3	4	5	6	7	8
11.6 - 15.0	0	1	2	3	4	5	6	7	8	8
15.1 - 26.6	1	2	3	4	5	6	7	8	8	8

Table 2. Severity values calculated from accumulation of rainfall in millimeters (mm) over a 24-hour period.

Amount of rainfall (mm)	Severity values
0.1 to 5.0	0
5.1 to 10.0	1
10.1 to 15.0	2
15.1 to 20.0	3
20.1 to above	4

DAYCAST was designed in this way because of experience with a government sponsored cull burial program administered in Prince Edward Island between 1953 and 1976. Observations of blight epidemics during this period seemed to show that disease onset was delayed and the ultimate severity of the epidemic reduced as primary inoculum density decreased. If lowering primary inoculum levels affects disease progress (3, 25), it is also possible that the use of efficient controls within growing regions affects disease progress by continuously interfering with natural increases in inoculum density during the entire growing season. Therefore, spray interval recommendations generated by the DAYCAST program are calculated both from severity value totals and from disease status reports (Table 3).

Categories for disease status used in the model are defined in the following way (Table 3). Category 1 occurs only when there is no evidence of blight in any quadrat within a large commercial or experimental field. Disease status increases to category 2 if a disease locus is seen in any examined quadrat, to category 3 when disease loci become lightly scattered or disease as severe as 1% can be seen in some quadrats. Disease status advances to category 4 if 1% disease is observed frequently and to category 5 if more than 1% disease becomes common.

IMPLEMENTING DAYCAST IN INDUSTRY:

DAYCAST operates as a regional forecast in New Brunswick, Prince Edward Island, and Nova Scotia (2, 7, 8). Hygrothermographs are placed in the center of growing regions, each approximately 25 to 30 km^2 by mid June. Severity value totals from each local weather station are combined with matching disease status reports to provide daily forecasts for each region. Experienced potato inspectors check fields within regions daily for evidence of virus mosaic, potato spindle tuber viroid, black-leg, ring-rot and late blight, so disease status information is always up-to-date. Forecasts are published in local newspapers, are broadcast over local radio or television stations or are recorded in

Table 3. Spray interval recommendations generated by severity value totals and disease status

Disease Status	Seven-day severity value totals							
	0-1	2	3	4	5	6	7	8
(1) No disease	N[a]	N	14[b]	10	10	10	7	7
(2) Disease loci sparse	10	10	10	10	7	7	7	7
(3) Disease slight	10	10	10	7	7	7	7	7
(4) Disease moderate	7	7	7	7	7	7	5	5
(5) Disease severe	7	7	5	5	5	5	5	5

[a] Fungicide application is not required
[b] Apply fungicides at intervals indicated (days)

English and French on toll-free telephone lines. The service is offered from July 1 to August 31 presently but may be offered in September in some provinces in the future.

TESTING THE ACCURACY OF DAYCAST:

Because of growing concern in industry over DAYCAST's accuracy, field plots were established between 1984 and 1986 to test its recommendations. In 1984, two large plots each 1 ha in area were sub-divided into 36 small quadrats each 3 by 4m. Russet Burbank was chosen for this trial because it is very susceptible. One large plot was sprayed according to DAYCAST's recommendations and the other was left unsprayed. Each quadrat was examined for symptoms of late blight every 5 to 14 days during the months of July, August and September. When disease affected less than 1% of the quadrat, the numbers of lesions were recorded but were not used to establish apparent infection rates (r). When disease severity was 1% or greater, Horsfall-Barratt ratings were assigned to each of 4 rows in each quadrat. Ratings then were transformed into proportions diseased for each row (9, 10, 36). Means for each quadrat then were calculated.

A logit transformation (D) of disease proportions (X) less than 0.5 was obtained for each small plot from the equation $D = \ln(X/1-X)$. Slopes of regression equations $D = a + rt$, relating D to time (t) in days, provided estimates of apparent infection rates (r) for each plot (9, 10, 12, 36). A "zero time" value for D was obtained by regressing all points against time and this in turn was used for $t=0$, for all calculations (10). The r values then were subjected to an analysis of variance and means compared with a protected LSD test. The mean r values then were used to estimate the amount of disease present in each large plot at harvest.

Results from the 1984 trial showed that the forecast provided recommendations which, when followed, gave good disease control on a very susceptible cultivar in a season with rapid epidemic development (Table 4). Therefore, in 1985 and 1986, trials were established to determine if a susceptible cultivar, Keswick and a more resistant one, Belleisle could be sprayed less frequently than the forecast recommended.

Replicated plots of Keswick and Belleisle were planted in randomized complete block designs in the first week of June in 1985 and 1986. Small plots had 4 rows 5 m in length. Plots were spaced 3-5 m apart. All rows were treated. Experimental blocks each had two cultivars and six spray treatments. Six plots were assigned to each cultivar randomly in each block, then treatments were assigned to the cultivars. Each block was designed independently. The large block design was replicated six times each season. Race 1, 2, 3, 4 was established on 3 leaflets of 6 greenhouse grown plants. Plants then were introduced into the center of each block during the third week in July each season. No inoculum, however, was placed into the 1984 field plots.

Weather stations were established each season next to experimental plots. Air temperature and periods of relative humidity above 90% were recorded with both a hygrothermograph and CR21 micrologger (Campbell Scientific Ltd., Logan, Utah). Instruments were checked weekly and hygrothermographs recalibrated as needed. Weather data from the station and assessments of disease were used to calculate the daily forecast as described previously (Tables 1, 2, 3).

Fungicides were applied at recommended rates each season. In 1984, fentin hydroxide was applied at 0.3 kg/ha ai with a tractor drawn trailing-boom sprayer. In 1985 and 1986, mancozeb was applied at 2.2 kg/ha ai with a backpack Solo sprayer (SOLO Kleinmotoren GmBH, Sindelfingen, W. Germany). In 1985 and 1986, plots were sprayed every 7 days, at intervals generated by the forecast, or at intervals 3, 7 and 14 days longer than the forecast or were left unsprayed.

In 1985 and 1986, plots were assessed and apparent infection rates (r) calculated as described previously. The r values, however, were subjected to a three-factor analysis of variance and then means for treatments and cultivars were compared using a protected LSD test at p=0.05 (Table 4).

Table 4. **Apparent infection rates (r) in trials designed to test DAYCAST**

Treatment Regime	No. of Sprays Applied	Mean Apparent Infection Rate (Days $^{-1}$) Russet Burbank
Check	0	0.211 a*
Forecast interval + 0 days	12	0.139 b

Treatment Regime	No. of Sprays Applied	Two Season Mean Apparent Infection Rate (Day^{-1})		
		Keswick	Belleisle	Average
Check	0	0.164	0.150	0.157 e**
Forecast interval + 14 days	4	0.162	0.146	0.154 e
Forecast interval + 7 days	6	0.158	0.147	0.152 e
Forecast interval + 3 days	9	0.154	0.139	0.147 f
Forecast interval + 0 days	11	0.156	0.140	0.148 f
Every 7 days	11	0.157	0.136	0.147 f
Cultivar Mean			0.159 x**	0.143 y

* Apparent infection rates followed by the same letter in a given column or row do not differ according to a protected LSD test at P = 0.01.

** The protected LSD test is significant at P = 0.05.

VALIDITY OF DAYCAST'S RECOMMENDATIONS:

Equations generated from 1984 field data were D= -18.0 + 0.139t for sprayed and D= -18.0 + 0.211t for unsprayed plots, where June 12 was "time zero" and -18.0 the intercept value for D. If 5% disease (D= -2.9) is considered an economically acceptable level for disease at top kill time, it would take 126 days in sprayed but only 72 days in unsprayed plots to reach this level. Corresponding dates are September 26 for sprayed and August 23 for unsprayed plots. In a season with relatively rapid epidemic development, spraying according to DAYCAST provided a susceptible cultivar, Russet Burbank, with an acceptable level of control. This finding agrees with reports made earlier for other similar late blight forecasting models (4, 5, 22, 23).

In 1985 and 1986 field trials, r values did not differ in plot sprayed every 7 days, in those sprayed according to the forecast or at intervals 3 days longer than the forecast (Table 4). Plots sprayed at intervals longer by 7 days or more, however, had r values that did not differ from the unsprayed checks. It should be pointed out that epidemic development was so similar in 1985 and 1986 that, for brevity, a mean response over 2 seasons is presented in further discussions of treatments.

The 2 season overall equation for the first treatment group, i.e. the group sprayed most frequently, was D= -18.0 + 0.148t where June 12 was "time zero" and -18.0 the D intercept. The corresponding equation for the check group was D= -18.0 + 0.157t. Dates corresponding to 5% disease were September 22 for the first treatment group and September 16 for the check group. In 1985 and 1986, differences between the two treatment groups, although statistically significant, were of such a small magnitude that they were of no practical importance. If top killers had been applied to any of these plots in the second or third week of September, yield losses and tuber infections would have been negligible, provided that the vines were completely dead and dry at harvest. On the other hand, if vines were improperly top killed, tuber infection might have become a problem.

In spite of possible interplot interference, experiments did accurately represent epidemic development in commercial fields each season. In 1984, late blight was reported by inspectors by July 12. The disease then became a serious problem in many growing areas. In 1985 and 1986, late blight was not seen until the second week of August in many locations and did not become serious in either season.

Cultivar differences were well defined and were consistent in field plots. The r values on Keswick and Belleisle differed statistically at a highly significant level. Differences in r were greater between cultivars than between spray treatment groups. Estimated dates corresponding to 5% disease were September 12 for unsprayed Keswick and September 22 for unsprayed Belleisle. For comparison, regularly sprayed Keswick showed 5% disease on September 17. Cultivar differences have been shown for both early (9, 10) and late (5, 6, 18) blights on potato. If the program is to be made cost effective, it must be modified to consider inherited levels of disease resistance.

CONCLUDING REMARKS:

DAYCAST's recommendations are cost ineffective for several reasons. The model does not consider that effects from blight favorable weather accumulate over the entire growing season. It is probable that the ultimate severity of the disease depends not only on how frequently blight favorable periods occur but also on how widely they are separated from each other in time. Clearly, there is a need to develop a new system for calculating severity values. This system should be based on cumulative weather data and should be reconstructed using some form of risk assessment analysis. It is quite probable that including disease status information in the model is a sound approach but its validity cannot be checked until the first part of the model is amended.

Since cultivars do vary in their response to late blight infection, it is necessary to modify this model accordingly. More field work is needed, however, before reliable and cost effective changes can be made. Commercially grown cultivars could be grouped into 3 or 4 categories and a representative from each tested more extensively. Representative cultivars should be tested in seasons with rapid, moderate and slow epidemic development to determine how frequently each needs to be sprayed in different conditions. Also, the stability of the disease resistance needs to be tested.

Reporting the location and severity of late blight is in itself valuable to the growers. Informing growers that weather conditions are favorable or unfavorable to blight infection also is of benefit but the spray interval recommendations provided by the forecast may or may not be accurate. It should be possible to improve DAYCAST given our more modern understanding of epidemiological methods (5, 12, 23, 36).

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THE CONTROL OF FUNGAL DISEASES OF POTATOES (EXCEPT LATE BLIGHT)

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ABSTRACT

The most frequent fungal potato diseases encountered in Canada were reviewed from the standpoint of control methods recently developed through research contributions of Canadian scientists. Very few scientific papers from Canadian sources were found in the literature from the last ten years on the specific topic of control. Wart, early blight, Verticillium wilt and black scurf seem to have been the major subjects of control oriented research. In addition, the research notes contained in the Canadian Horticultural Council Annual Report from 1981 through 1985 reveal that trials are currently carried out in Prince Edward Island and, to a lesser extent, in Quebec on chemical control of Verticillium wilt, fusarial rots and Rhizoctonia. Chemical control of Fusarium and Phoma rots in storage is under investigation in New Brunswick. Sporadic reports from Nova Scotia and Alberta deal with the chemical control of seed piece decay.

RESUME

La contribution des chercheurs scientifiques canadiens au développement de méthodes de répression des maladies fongiques de la pomme de terre les plus fréquemment rencontrées au Canada fait l'objet de cette revue. La littérature scientifique des dix dernières années renferme très peu d'articles de source canadienne portant spécifiquement sur la répression des maladies. La galle verruqueuse, la brûlure hâtive, le flétrissement verticillien et la rhizoctonie ont été les principaux sujets de la recherche orientée vers la répression. De plus, les rapports annuels du Conseil Canadien de l'Horticulture de 1981 à 1985 révèlent que des essais de répression chimique du flétrissement verticillien, des pourritures fusariennes et de la rhizoctonie sont effectuées à l'Ile du Prince Edouard et, à un degré moindre, au Québec. Des essais de répression chimique des pourritures phoméenne et fusarienne en entrepôt se déroulent au Nouveau Brunswick. Quelques rapports émanant de l'Alberta et de la Nouvelle Ecosse traitent de la répression chimique de la pourriture des plantons.

INTRODUCTION

Many kinds of organisms serve to maintain or break the balance of Nature. Man, for example, often disrupts this balance. Intensive potato growing brings the necessity for protection againts what are called pests, including fungi. There are about 60,000 species of fungi on earth and, like man, they are hopefully here to stay. Protection of potatoes must therefore be accomplished through judicious control rather than destruction of fungi. Fungi can cause some 40 diseases to the potato around the world. Aside from late blight, caused by Phytophthora infestans (Mont.) de Bary, there are about 12 fungal diseases which may attack potatoes in Canada.

The purpose of this paper is to review briefly some of these diseases in order to give a broad view of the situation with respect to their relative importance and to the research efforts that are presently devoted to them for satisfactory control and adequate protection of potatoes in Canada. Table 1 shows the diseases and their respective causal agent(s) which were included in the review.

Table 1. Review of some fungal diseases of potato other than late blight

Disease	Causal agents
Early blight	*Alternaria solani* (Freis.) Kessler
Fusarium dry rots and wilts	*Fusarium* spp.
Gangrene	*Phoma exigua* Desm.
Leak	*Pythium* spp.
Pink rot	*Phytophthora erythroseptica* Pethybr.
Powdery scab	*Spongospora subterranea* (Wallr.) Lagerh.
Rhizoctonia canker & Black scurf	*Rhizoctonia solani* Kühn
Silver scurf	*Helminthosporium atrovirens* Dur. & Mont.
Skin spot	*Polyscytatum pustulans* (Owen & Wakef) M.B. Ellis
Verticillium wilt	*Verticillium albo-atrum* Reinke & Berk *Verticillium dahliae* Kleb.
Wart	*Synchytrium endobioticum* (Schilb.) Perc.

The following three data banks were used to retrieve the information on control of fungal potato diseases: CAB Abstracts, AGRICOLA and ICAR.

It is hoped that this obviously incomplete review will generate fruitful exchanges and discussion on the opportunity of allocating additional resources or reallocating resources for research on control of fungal potato diseases in Canada. Table 2 illustrates the number of papers published on the control of eleven potato diseases (except late blight) between 1973 and 1986.

Table 2. Number and country of origin of papers published on control on 11 fungal potato diseases except late blight (CAB Abstracts 1973 - 1986/Oct.)

Disease	Canada	Australia and India	Israel Egypt France	The Nether-lands	Ireland and UK	SA and USA	Total
Early blight	2	3	1		1	6	13
Fusarium rots	2				1		3
Leak							0
Pink rot						1	1
Gangrene					8		8
Powdery scab		2			3		5
Rhizoctonia	1	2	3	8	12	6	32
Silver scurf					3		3
Skin spot					1		1
Verticil. wilt	3		2		1		6
Wart	2				1		3

THE CONTROL OF LEAK

Leak or watery wound rot can occur sporadically wherever potatoes are grown. Only potato tubers are affected by this disease. The causal agent enters through wounds. This disease may strike when immature tubers are bruised when harvested during hot, dry weather. Avoiding bruises is essential to preventing the disease.

Apparently, no research results have been published on the control of this disease over the last fifteen years either in Canada or elsewhere.

THE CONTROL OF SKIN SPOT

Skin spot may be a devastating disease following planting. Sporadic unofficial reports have been heard on the occurence of this disease in Canada over the last ten years. However, skin spot has seemingly not been of sufficient economical importance to alarm government officials or even plant pathologists.

It is possible that the increasing practice of treating potatoes before storage with thiabendazole is contributing significantly to prevent the spread of this disease because thiabendazole penetrates and prevents sporulation of the fungus.

THE CONTROL OF POWDERY SCAB

Powdery scab lesions may serve as infection courts for late blight and number of wound pathogens. The causal organism is difficult to work with; its resting spores, or cysts, may persist in the soil for up to six years and survive passage through the digestive tracts of animals. It is a vector of the potato mop-top virus. Some dicotyledons, monocolyledons and gymnosperms are among its hosts. No completely adequate control measures have been developed so far and, apparently, no Canadian scientist is working on this topic at the present time. Considerable knowledge is needed on the epidemiology of powdery scab, especially with respect to the effect of liming.

THE CONTROL OF PINK ROT

The pink rot disease of potatoes is so called because, when partially rotted tubers are cut, the internal tissue, which is spongy or rubbery, odorless and cream colored, changes within 20 minutes to salmon pink upon exposure to air. The disease is most frequently observed in mature plants approaching harvest. It is most severe in wet and warm soils. It is recommended to avoid soils with poor drainage and excessive irrigation late in the growing season.

Very little information is available on the control of this disease and, to my knowledge, no research is being conducted on this topic in Canada at the present time. In Peru, pink rot has been a serious problem in the maintenance of the germplasm collection at CIP's experimental station in Huancayo. It annually causes serious loss of germplasm accessions, particularly of diploid cultivars. Torres, Martin and Henfling (12) have shown that effective chemical control of pink rot of potato can be achieved with the combined use of dazomet 98% and metalaxyl 5% applied to soil only.

THE CONTROL OF GANGRENE

This disease causes small dark depressions in the tuber skin and they may enlarge to form "thumb-mark" lesions. Tuber infection may take place through eyes and lenticels but wounding is often responsible for most of the damage resulting from gangrene. Gangrene occurs in most northern European countries. During the last five years, there have been unofficial reports that gangrene is increasing in Canada.

Research papers on control of gangrene come from the UK and Ireland. None were found from Canadian authors. Mist sprays of thiabendazole within three weeks of harvest are recommended for control. In addition, according to J.R. Walsh (N.B. Dept. of Agriculture, Florenceville, N.B., personal communication), Phoma spp. was not identified in any of the samples of New Brunswick commercially grown Shepody and Russet Burbank potatoes in a chemical control trial in storage with thiabendazole, imazalil and thiophanate methyl.

THE CONTROL OF SILVER SCURF

Silver scurf is a seed-transmitted disease of potato tubers. Soil transmission may also occur. Infection takes place before harvest and disease continues to increase in storage. Use of disease free seed is the best control measure. However, seed treatment with benomyl is effective in controlling the disease. It is also recommended to harvest the tubers as soom as they are mature.

In Northern Britain, a combination of thiabendazole and 2 - aminobutane sprayed on tubers after harvest provided good control. Benomyl, imazilil, thiophanate methyl are also said to give good results in post harvest treatments. One Canadian who published extensively on silver scurf in Jocelyn Santerre. No literature from Canadian sources has been found on the control of silver scurf over the period from 1972 up to the present. However, N.S. Wright (U.B.C., Vancouver, personal communication) recently demonstrated that thiabendazole applied as a spray prior to planting provides less efficient control of silver scurf than thiophanate methyl during the six months of the following storage season.

THE CONTROL OF FUSARIUM ROTS

A purposely small portion of this review is devoted to Fusarium rots and wilts. Yet, dry rots, for example, are probably the most widespread potato diseases around the world; for this reason, possibly, like the late blight disease, they are among the best known diseases in terms of host-pathogen relationships and epidemiology, despite the fact that they represent very complex disease systems since 12 species of _Fusarium_ were found in association with the porato (7).

Only chemical control is adequate to control _Fusarium_ dry rots (7). The use of good quality seed and wound prevention by appropriate handling are rewarding investments in the control on dry rots.

Control of _Fusarium_ wilts, which are favored by hot and dry weather can be maintained again by the use of good quality seed, proper cleaning and desinfection practices and by avoiding the buildup of inoculum resulting from continued potato production.

THE CONTROL OF EARLY BLIGHT

This disease is found world-wide. It destroys leaves and damages stems. Symptoms intergrade with those of verticillium wilt. Tubers are also attacked, especially if immature or wounded. No cultivar is immune to this disease but levels of filed resistance are available. Early season applications of fungicides before secondary inoculum is produced has little or no effect on the spread of the disease. Fungicides such as the dithiocarbamates, chlorothalonil and fentin hydroxide effectively control early blight on the foliage. Adequate fertilizers and elimination of residues contribue to low levels of this disease.

Barak, Edgington and Ripley (2) at the University of Guelph have demonstrated that foliar applications of metalaxyl, a systemic fungicide resulted in residue levels in potato tubers (2.5-12 mg/kg) which prevented decays due to Alternaria solani in storage. When after 4 months of storage the metalaxyl level had decreased to 8 mg/kg, the resistance was lost. This resistance was attributed to polyphenol oxidase, the activity of which was stimulated by the presence of metalaxyl in the tuber tissue. However, Platt (10) reported a reduction of early blight over a period of three years with mancozeb and chlorothalonil but not with metalaxyl.

Holley, Hofstra and Hall (6), a research team of the University of Guelph, related early blight damage to ozone injury. They found that ethylene diurea (EDU) protected potato foliage from visible injury due to ozone in laboratory and field experiments. When fentin hydroxide was combined with ethylene diurea, greater than additive response to the combination treatment was obtained compared to either single spray treatment. Since fentin hydroxide did not diminish ozone injury on potato leaves in controlled fumigations, but did reduce adaxial bronzing in the field, it is suggested that ozone lesions became colonized by A. solani under natural field conditions.

THE CONTROL OF WART

Potato wart is a very dangerous and economically important disease. It is destructive to potatoes and its causal agent can persist in soil for as long as 38 years. It has been recorded in Africa, Asia, Europe and North and South America. Worldwide control of spread is implemented through national and international quarantine legislation.

The disease was identified in Newfoundland in 1909. The federal government passed the Destructive Insect and Pest Act in 1910. The government of Newfoundland issued regulations for its control in 1916. In 1930, all potato imports in Canada had to be declared free from wart. Surveys were made in 1949, and later in 1955 through 1973. Intensive research was initiated aroung 1964 in Newfoundland. M. Hampson and K. Proudfoot have published and are presently conducting research which places them amond the leading scientists on potato wart in the world.

In a review paper, Hampson (4) pointed out the progress that has been accomplished in the control of wart by breeding resistant cultivars. Resistant cultivars are not sufficient by themselves to bring the wart disease under sufficient control to relieve the pressure of high risks for the potato industry in Canada (5). Moreover, chemical control has not been successful so far because it was either injurious to soil or plants.

Progress towards the solution of the potato wart problem is dependant upon a new emphasis on host-pathogen interactions. A metter understanding of infection parameters and of pathogenesis in terms of inoculum and incubation is necessary to provide a basis for development of more efficient control measures.

THE CONTROL OF RHIZOCTONIA CANKER AND BLACK SCURF

Rhizoctonia solani has a wide geographic distribution and a wide host range. It occurs on tubers as sclerotia and on plants which it damages in reducing quantity and quality of yields. It is a very serious disease. Incresasing awareness of its importance has brought about important economic losses due to rejection of infested seed lots. Rhizoctonia canker was said to be very difficult to control. However, when seed free from sclerotia in used, very little or no canker develops In many cases, however, control of black scurf is difficult.

One of the biggest difficulties in research to control black scurf economically is the measurement of the progeny tuber reaction to black scurf in response to control treatments. The variability associated with these measurements is so large that gigantic samples are needed. This difficulty may be reflected by the fact that more than 30 papers have been published on control of Rhizoctonia over the last 15 years. Extensive work has been done in the Netherlands on biological control through seed tuber inoculation with hyperparasitic fungi; however, practical applications of biological control are to be further sought. In the UK, tolclofos-methyl has given reliable and economic control of stem canker and black scurf when applied as a dust seed treatment prior to planting.

Types of reaction and levels of resistance to stem canker have been identified in some cultivars. Inheritance mechanisms are not known. With regard to black scurf, cultivar resistance still awaits demonstration. Infestation mechanisms are partly known on the basis of potato reaction to cultural methods (1). In Canada, black scurf of potatoes has been found to be caused by the anastomosis group 3, AG-3, of Rhizoctonia solani by Otrysko, Banville and Asselin (9). Present research at Laval University by this same group bears on biochemical host-parasite relationships with the purpose of finding what causes sclerotia to form on potato tubers. In Charlottetown, Platt, H.W. (Agric. Canada Res. Station, Charlottetown, P.E.I., personal communication) has done some work on viability and survival of sclerotia following chemical treatment of tubers. To summarize, even though chemicals such as thiabendazole, and tolclophos-methyl can in many instances achieve reliable and satisfactory control of Rhizoctonia, research is needed primarily to find economical means of controlling black scurf. In most cases, stem canker will not occur when seed is free from black scurf.

If all the money from all sources which was spent during the last 5 years because of the problems that black scurf caused between Canada and Uruguay alone was placed in a National Black Scurf Research Fund (NBSRF), the interest would be sufficient to support a nice annual research project.

THE CONTROL OF VERTICILLIUM WILT

Verticillium wilt is a fungal disease that can be seed borne or soil borne. The fungus enters the root system of the host, attacks the vascular system and causes wilting of the plant. It may be confused with other diseases which cause early maturity because it typically causes early senescence of the plants. Verticillium wilt apparently occurs wherever potatoes are grown. This disease is important in North America and in Canada. The disease can reduce table stock production by as much as 20%. In P.E.I. and New Brunswick, it was said to account for 2% of all seed crop rejections in 1982. During that same year, serious losses occured in Quebec in seed fields of Superior and in early table stock crop.

The control of this disease is complicated by the fact that two causal agents may be involved, that numerous common weeds are susceptible hosts, and that several nematodes increase incidence and severity of Verticillium wilt. They include planting highly susceptible cultivars such as Kennebec. Another important aspect of control is the control of spread of the disease. Indeed, many environmental conditions and some cultural methods may prevent the development of wilt but the absence of wilt is no guarantee that the causal agents will not be transmitted by seed to the next generation of tubers.

The following items should assist in providing some control of the disease.

Land for potato production that has legumes, corn, and some other crops in rotation with potatoes can maintain levels of the pathogen, if present.

Seed should be free of disease infection. Macroscopic symptoms on or in tubers or plants are the basis for rejection of certain seed lots for certification purposes. However, the absence of symptoms does not mean the crop is disease free.

Cultivation and hilling should be done early to produce a broad hill and prevent root and shoot damage.

Removal and burning of the previous potato crop debris eliminates a source of disease.

The use of nematicides and fungicides is recommended.

Seed tubers should be disinfected by a liquid chemical treatment before planting. This is because inoculum adhering to the surface of potato tubers is important in initiating wilt symptoms. Some chemicals such as methylthiophanate have given satisfactory control of wilt.

Other items which sould be taken into consideration in preventing spread on the disease are the date at which vines are killed in seed crops, the amount of applied nitrogen which in excess, can mask the disease symptoms on the plants, and the determination of the Verticillium species present in a field. This last item would help to establish disease severity potential and the most appropriate means of control.

Research on the control of Verticillium wilt of potatoes in Canada has been primarily done by scientists from P.E.I. and from Ontario. McKeen and Thorpe (8) reported that *v. albo-atrum* was considerably more pathogenic than *V. dahliae* in Ontario. In Southwestern Ontario, *V. dahliae* survives in soil but *V. albo-atrum* rarely overwinters. Busch et al (3) studied the effect of weeds on the value of rotation as a practical control for Verticillium wilt in Ontario. The authors suggested that, in Ontario, rotation would be of no value in controlling Verticillium wilt of potatoes.

At the present time, compared to the relative importance of this disease in Canada, little work is being done on the control of Verticillium wilt. Most recently, Platt (11) published a paper on varietal response of many of the major cultivars in production to current season infection and to internal seedborne disease transmission; B. Platt in P.E.I. and L. Tartier in Quebec are among the very few scientists currently devoting efforts to the control of verticillium wilt. To summarize, control of Verticillium wilt is very important to the Canadian potato industry. The lack of economical and efficient means of control and the losses which it annually causes would justify a well funded research program.

CONCLUSION

The use of good quality seed and wound prevention are the keys to control a number of tuber rots in storage and in the field at planting time. This measure can be aided by pre-storage or pre-planting chemical treatment of seed or soil. However, in the case of rhizoctonia canker for example, it is generally recognized that the use of healthy seed devoid of sclerotia makes chemical seed treatment superfluous.

Three to four year rotations are often recommended as a control method against many fungal diseases of potatoes. Farmers are sometimes reluctant to follow such recommendations. The cost of land, the lack of profitable intermediate crops, the lack of information on the effect of new soil manuring and amending practices on the quality of the potato crop and on the incidence of soil borne diseases are among the reasons that are put forward to question the recommendations of rotations.

The necessity to preserve the environment and to protect Canadian soils from deteriorating logically precedes our capacity of maintaining and improving the production of high quality potatoes in Canada. It is suggested that integrated control programs against fungal diseases of potatoes should be constituted of projects where soil management and rotation practices serve as a basis for other parameters, including economical ones. Furthermore, while the continuous evaluation of chemical control methods is needed to make them more efficient and economical, it is also suggested that research emphasis should be placed on epidemiology and host-parasite relationships. Host-parasite relationships constitute the core of plant pathology. The knowledge or ignorance of what is going on at that level determines the potential and chance of developing better control methods, while direct and indirect costs of pesticides should always be taken into account (Fig. 1).

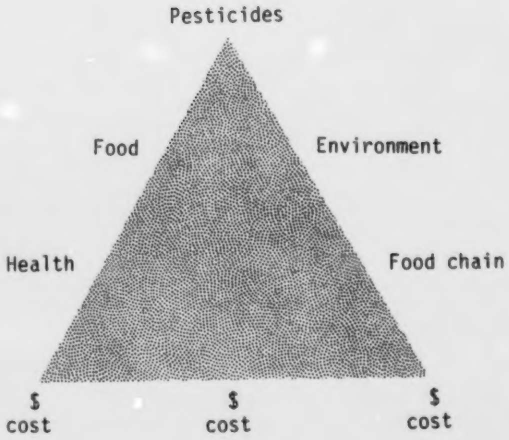
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Fig. 1. Direct and indirect costs of pesticides

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CONTROL OF VIROID AND CONTACT TRANSMITTED VIRUS DISEASES

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ABSTRACT

Control measures for each pathogen are best based on knowledge of its mode of transmission, survival in propagating hosts and inoculum sources. Attempts are made to identify the factors influencing pathogens' spread in the field and persistence in the propagating material, so that control measures may be applied to minimize these. Irrespective of the intrinsic nature of the pathogens, some common epidemiological measures can be applied to minimize their spread. This is illustrated in this presentation. Thus, the potato spindle tuber viroid, potato virus S and potato virus X will be considered here together.

RÉSUMÉ

Idéalement les mesures de controlê des pathogènes se basent sur une bonne compréhension du mode de transmission de chacun, sur une connaissance de la durée de survie chez l' hôte et des sources d' inoculation. Ce texte essaie d' identifier les facteurs qui influencent la dispersion des pathogènes dans le champ et leur persistence dans le matériel de propagation dans le but de développer des mesures de contrôle pour les enrayer. Quelle que soit la nature intrinsèque des pathogènes, certaines mesures du contrôle épidemiologiques s' appliquent à la gérance de tous les pathogènes. Ceci est illustré dans cette présentation. Ainsi, le viroide de la filosité ainsi que les virus S et X de la pomme de terre seront considérés ensemble dans cet exposé.

NATURE OF PATHOGENS

Potato spindle tuber viroid (PSTV). Potato spindle tuber viroid is a low-molecular weight ribonucleic acid (10,45) devoid of the protein coat commonly associated with plant viruses. The ribonucleic acid molecule is a covalently closed circular structure (34) of 359 nucleotides (17). Viroid molecules appear as short rods in their native state, and when they are denatured appear as open circles (34). PSTV exists as mild, intermediate and severe strains and all have the same length of nucleotides, but differ in their sequences with minor changes. Depending on strains, it can reduce potato tuber yield from 16 to 65% (51). PSTV has a wide host range (40), and mild strains predominate in the field (50).

Potato virus S (PVS). It is a RNA containing virus with straight to slightly curved filamentous particles of about 650 x 12 nm (7). It causes few or no symptoms and is carried by many cultivated and wild potato varieties. It decreases yields 3-20% and is transmitted to a limited number of plant species. It has world-wide distribution and some isolates may be aphid-transmissible (see Singh and Boiteau, these proceedings).

The typical North American and European isolate of PVS causes the development of local lesions in Chenopodium species, while an Andean isolate causes the development of systemic symptoms in Chenopodium species (C. quinoa, C. amaranticolor, C. rubrum). The Andean isolate sometimes causes chlorosis and bronzing of leaves in European potato cultivars (33) but is carried symptomlessly in Red La Soda potatoes (52). The Andean strain is readily transmitted by aphids (52).

Potato virus X (PVX). It is a RNA-containing virus with elongated particles of about 515 nm. It is readily transmitted by inoculation of sap, and is widely distributed in potato-growing areas of the world. It causes mild mosaic of potato and can reduce yield alone or in combination with other potato viruses (30,59).

On the basis of the reactions to different potato cultivars, four strains of PVX are recognized (30). Recently a strain from the Andean region has been described (27), which differs from the previously existing strains in infecting PVX-immune cultivars like Saco, Saphir and USDA seedling 41956. The Andean strain is also carried symptomlessly in Gomphrena globosa, an indicator plant widely used for indexing PVX (27).

DISTRIBUTION OF VIROID/VIRUSES IN THE FIELD IN 1969-70

A survey of PSTV during 1970 in tablestock fields in New Brunswick showed that the distribution of the viroid differed according to potato cultivars. For example, Russet Burbank contained 4.6%, Kennebec 3.3% and Katahdin 2.5% of PSTV (Table I). Another survey a year earlier had shown that mild strains were recovered in 92% of samples against 8% for the severe strain (50) (Table II). Mild strains reduced yields up to 16-24% (Table III) (51).

Most potato cultivars were infected with potato viruses S and X in the mid-sixties (53). Therefore, the specific distribution of these viruses was not possible to study until 1969-70, when both viruses were eradicated from potato plants by thermotherapy and axillary bud culture (53). It was observed in 1972 that when PVX and PVS-free potatoes were multiplied for three years at an Elite seed farm in Prince Edward Island where virus-infected potatoes were also grown, approximately 10% of the plants became reinfected with both viruses (21). However, when the same virus-free potatoes were multiplied at a private farm in the absence of virus-infected potatoes, all remained free from PVX, but some became infected with PVS (21) (Table IV). Similar observations were made by workers in the U.S.A. in 1980. In one study, 59% and 70% of plants were infected with PVS, while 19% and 55% of plants were infected with PVX after one and 3 years of field growth of virus-free potatoes (18). These studies pointed out that the reinfection rate was very rapid for PVS but slower for PVX.

TABLE I

PER CENT OF PLANTS INFECTED WITH PSTV IN TABLESTOCK FIELDS, NEW BRUNSWICK, CANADA, 1970[a]

Cultivars	No. of fields	Per cent PSTV	Average per cent
Kennebec	26	0,0.3,0.3,0.6,0.6,0.7,0.7.0.9, 1.0,1.4,1.4,1.8,2.3,2.5,3.1, 3.6,3.9,4.3,4.8,5.8,6.4,6.8, 7.4,7.8,16.6[b]	3.3
Katahdin	16	0,0,0,0.1,0.2,0.5,1.6,1.6, 2.2,2.7,4.2,4.6,5.0,5.3,5.9, 6.0	2.5
Russet Burbank	38	0.1,0.2,0.2,0.5,0.5,0.5,0.6, 0.6,0.7,1.0,1.4,1.5,1.6,1.7, 1.7,1.7,2.6,2.8,3.1,3.3,3.6, 4.6,4.8,4.8,5.0,5.6,5.7,5.7, 7.0,8.2,9.4,10.0,10.8,10.8, 11.8,12.3,14.4[b],16.5[b]	4.6

[a] Based on reference #51.

[b] Fields planted for 10 years continuously with the same seed.

TABLE II

MILD AND SEVERE STRAINS OF PSTV FROM TABLESTOCK FIELDS OF EASTERN CANADA, 1969[a]

Province	Cultivars	No. of fields	PSTV Strains Mild	PSTV Strains Severe
Quebec	Kennebec	5	33	5
	Keswick	2	8	2
New Brunswick	Kennebec	4	29	10
	Russet Burbank	5	167	4
Prince Edward Island	Kennebec	2	12	2
	Russet Burbank	2	13	1
	Sebago	2	19	2
Newfoundland	Pink Pearl	1	9	1
Total		23	290	27

[a] Based on reference #50.

TABLE III

YIELD OF HEALTHY SACO POTATOES COMPARED WITH THAT OF SACO INFECTED WITH 3 DIFFERENT ISOLATES OF MILD AND ONE ISOLATE OF SEVERE PSTV, FREDERICTON, CANADA[a]

Seed lot - viroid sources	Yield (lbs)/plot	Per cent loss
1. Mild PSTV - K.H. Fernow	38.3	24.3
2. Mild PSTV - K.H. Fernow	41.2	16.6
3. Mild PSTV - P.E.I., Canada	38.4	24.1
4. Severe PSTV - Maine, U.S.A.	18.4	63.6
5. Healthy	50.6	--

[a]Based on reference #51.

TABLE IV

REINFECTION OF VIRUS-FREE POTATOES WITH PVS AND PVX AFTER THREE YEARS ON FARMS WITH OR WITHOUT VIRUS-INFECTED SOURCES[a]

	With virus sources		Without virus sources	
	Percent infection		Percent infection	
Cultivars	PVS	PVX	PVS	PVX
Katahdin	8	6	0	0
Kennebec	10	9	-	-
Sebago	12	9	1	0
Russet Burbank	8	7	4	0
Red Pontiac	-	-	8	0
Green Mountain	-	-	8	0
Irish Cobbler	10	9	-	-

[a]Based on reference #21.

TABLE V

VARIOUS METHODS OF FIELD TRANSMISSION RECORDED FOR VIRUSES AND VIROIDS

Method of transmission	Viruses/viroids[a] PVS	PVX	PSTV
1. Contact of infected to healthy leaves	+19	+20	+35
2. Contaminated cutting knives	+12	+22	+13
3. Contaminated tuber sprout contact		+8	+9
4. "Switching" with infective vines			+25
5. Contact of infective seed-piece			+13
6. Use of picker-planters			+16
7. Contaminated tractor wheels		+32	+25
8. Contaminated cultivating and hilling equipment		+23	+23
9. Clothing and animal fur		+55	
10. Feeding of grasshoppers		+56	+14
11. True potato seed			+38

[a] Indicates reference # under literature cited.

TABLE VI

RETENTION OF INFECTIOUS VIRUSES AND VIROIDS ON VARIOUS SURFACES AND MATERIALS

Surfaces/materials	Retention periods of viruses/viroids (hours) PVS[a]	PVX[b]	PSTV
Painted wood	–	6	–
Unpainted wood	0	3	–
Iron or aluminum foil	7	3	–
Rubber	25	3	–
Jute or burlap	0	6	–
Cotton	–	6	–
Leather	0	–	–
Soil	0	24	–
Human skin	–	3	–
Infective sap at room temperature (22°C)	120	120	–
Freeze-dried leaf powder at 22-27°C	–	–	6 years[c]
True potato seeds			10-12 years[d]

[a,b,c,d], are reference #12,58,48 and 15, respectively.

TABLE VII

SURVEY AND DETECTION OF PSTV IN TABLESTOCK FIELDS, NEW BRUNSWICK, CANADA, 1984

Cultivar	Class of planted seed	No. of fields	PSTV detection	
			Bioassay[a]	cDNA[b]
Kennebec	EII[d]	1	0/5[c]	0/5
Kennebec	EIII	1	0/5	0/5
Kennebec	F	4	0/20	0/20
Kennebec	C	2	0/10	0/10
Russet Burbank	EIII	20	0/100	0/100
Russet Burbank	F	27	0/135	0/135
Russet Burbank	C	6	0/30	0/30
Shepody	EIII	6	0/30	0/30
Shepody	F	9	0/45	0/45
Shepody	C	8	0/40	0/40
Superior	EII	1	0/5	0/5
Superior	EIII	3	0/15	0/15
Superior	F	8	0/40	0/40
Superior	C	7	0/35	0/35
PSTV controls[e]	-	103	102/103	98/103

[a] Bioassay on Solanum berthaultii plants.
[b] Complementary DNA - hybridization, using Agdia Inc. kit.
[c] From each field 5 samples consisting of 100 leaflets each were used to extract nucleic acid.
[d] Classes of seeds: Elite II, Elite III, Foundation, Certified.
[e] For each field 1 PSTV control was included. The control consisted of 1 PSTV-infected leaflet combined with 99 leaflets from healthy plants of the same cultivar being surveyed in the field.

Means of field infection and spread. High rates of infections were observed for PSTV, PVX and PVS by contact with contaminated seed, machinery and tools (Table IV). For example, contact of bruised tuber sprouts with PSTV infective sap gave 50% transmission (9); brushing healthy potato vines with PSTV-diseased vines gave 80-100% infection (25); PSTV-contaminated cultivating and hilling equipment gave 31 to 65% transmission (23). Similarly, a high rate of infection ranging from 54 to 93% of PVX was obtained by cultivating and hilling equipment (23), and use of contaminated knives gave 25 to 97% infection of PVS in different cultivars (12) (Table V).

Survival of viroids and viruses on various surfaces and materials. For the highly infectious agents like PSTV, PVS and PVX, the contact of surfaces like contaminated machinery, storage and grading facilities, sacks and clothing may result in spread of pathogens to the healthy stocks. Studies (12,58) have shown that surfaces like painted or unpainted wood, iron, rubber, jute or burlap, cotton, soil and human skin, can retain infectious PVS or PVX for various periods (Table VI). Although no information of the same sort is available for PSTV, it has been shown to remain infective in freeze-dried leaves (48) and true potato seeds (15) for 6-12 years.

Control of viroids and viruses in Canada. Surveys of PSTV in New Brunswick in 1985 (46) showed that viroid incidence in potato seed crops decreased to a point where it could not be detected by visual observation (Fig. 1). On the basis of an average of 1988 fields or 10,565.6 hectares per year of seed potato production in New Brunswick, it was noted that PSTV incidence in various cultivars declined steadily from 1969 to 1980 (46). Since 1980, no PSTV has been observed. Another survey of tablestock fields and attempted detection of viroid by various methods of detection failed to show the presence of PSTV in any of 51,500 leaf samples tested (47) (Table VII).

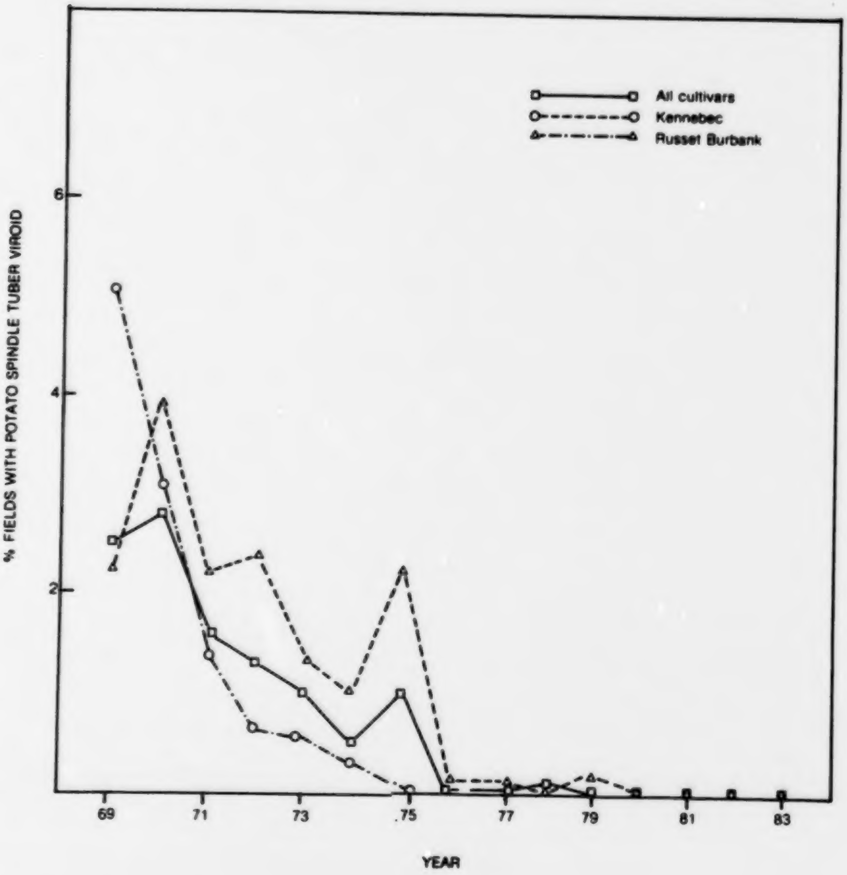
Surveys in 1985 in British Columbia (60) showed that PVX and PVS were under virtually complete control on the 21 Elite and Foundation seed farms in Pemberton, on one farm in East Kootenay and on 3 farms in Cariboo. Virus-free seeds of 16 cultivars from Pemberton and Cariboo being grown on 16 Foundation and Certified seed farms in the lower Fraser Valley, Okanagan-Kootenay area and on Vancouver Island produced crops in which neither virus was present. However, two cultivars from Cariboo, which were partially infected with PVS, produced crops in which virus incidence increased nearly two-fold (60).

THE REASONS FOR THE DECREASE OF PSTV, PVS AND PVX

From the discussion above, it is clear that highly infectious pathogens like spindle tuber viroid and latent viruses S and X, which were prevalent in most fields during 1969-70, had decreased by the mid-1980s. The control of these pathogens was achieved through the concerted effort of several programs aimed at controlling potato pathogens in general. The programs are briefly described below.

LEGEND FOR FIGURES

Figure 1 Percentage of fields with potato spindle tuber viroid from 1969 to 1983, New Brunswick, Canada.



A. **Establishment of Elite Seed Farms.** In the mid-sixties, seed farms were established in each province in an attempt to produce and supply to Elite seed growers the highest quality seed. These seed farms were staffed with personnel experienced in the control and detection of bacterial, viral and viroidal diseases, as well as having facilities to isolate the fields, to perform technical procedures, and to restrict the movement of unwanted potatoes.

B. **Production of virus-free nuclear stock.** In 1968-70 the potato cultivars which were almost 100% infected with latent viruses S and X were freed of these viruses by thermotherapy and meristem culture (53). A few plants were also freed from PSTV infection (54). The greatest impact of this program was that it became standard practice to use the clones which had been derived through the virus-freeing procedures for multiplication at provincial Elite seed farms. In the process, these clones were tested for freedom from bacterial, viral and viroid pathogens. Newly released cultivars from a potato breeding program were required to pass through the virus-freeing procedure before their seed was available to growers.

C. **Development of sensitive detection methods.** Canadian seed improvement programs are constantly striving to upgrade the detection procedures for pathogens such as PSTV and viruses. For PSTV, the tomato-cross protection test was made more effective by the use of RNA extracts (44), the search for a tomato cv. developing diagnostic symptoms with mild PSTV was made (37), and efforts were made to improve the efficiency of indicator plants by improving the nutritional requirement for symptom enhancement. Additionally, local lesion (39,40) or systemic host plants were reported (43). The first biochemical test for viroid detection, based on mobility through polyacrylamide gels during electrophoresis, was developed in Canada (29) and its further improvement using tomato as an intermediate host for increasing the viroid concentration was also described (28). The suitability of plant parts (41), the tissue type, and the temperature (42) were further studied to make the diagnosis as sensitive as possible. Highly sensitive "Return" gel electrophoresis (36) and dot-blot (31) techniques are being developed (Singh, unpublished). For potato viruses, use of the highly sensitive ELISA (enzyme-linked immunosorbent assay) has been made (24,49,57), which is more sensitive (11) than the previously used latex test. With ELISA, one infected plant in 1000 has been detected (26).

D. **New Federal certification regulations introduced in 1970.** New regulations, which required Elite seed to be grown from virus-free cuttings, plants, or tubers, were introduced in 1970 (2). These regulations further required that all Elite I, II, and 10% of the Elite III seed be planted in tuber units and be inspected three times during the growing season. The potatoes grown in each category automatically drop a level the following year. These regulations thus constituted a "Flush-through" system where the virus/viroid-free tubers entered seed production as pre-Elite in year 1 and would be out of the growing system after 6 years. This removal of seed tubers from the system within 7 years reduced the buildup of diseases, particularly those which do not have aerial vectors. Thus, PSTV and PVX were successfully controlled. PVS, which may have aphid vectors, has been difficult to control.

E. **Zero tolerance for PSTV.** Because of the reduction in PSTV and other diseases throughout Canada, the seed regulations were further strengthened in 1980 by proclaiming "zero tolerance" for PSTV in any seed potato field at the first, second or third inspection (5).

F. **PSTV testing by potato breeding programs.** PSTV has been known to be transmissible through the pollen and the true potato seeds (38). PSTV may contaminate new cvs. during their development through pollen or ovule transmission, and thus be perpetuated undetected. In the early 1970s, the potato breeding programs started testing parental material for PSTV prior to making crosses. Furthermore, potato breeders tried to make sure that new cultivars or advanced seedlings were free of PSTV before they were multiplied for regional trials or cultivar evaluation tests.

G. **Use of disinfectants for cutting knives and tools.** In order to prevent accidental spread of PSTV and viruses like PVS and PVX from tubers during cutting of seeds, the use of several chemical solutions are recommended. For PSTV use of 1-2% sodium hypochlorite (commercial bleach) is very effective in decontaminating knives, etc. (Singh, unpublished data). A thirty-second dip in calcium hydroxide, trisodium phosphate, or bentonite clay was effective in preventing knife transmission of PVX (32). Seventy per cent ethyl alcohol, alcohol plus flaming, copper sulphate, boiling water and washing the knife blade in a rapidly flowing stream of water also proved effective, but none exceeded the effectiveness of calcium hydroxide (32).

H. **Provincial potato disease eradication acts.** In order to reduce the buildup of bacterial, viral or viroidal diseases, several provinces passed acts governing movement of potatoes from one place to another, their planting, inspection, etc. (1,4). For example, the New Brunswick government passed the Potato Disease Eradication Act of 1979 (4) which included PSTV as a prescribed disease. As a prescribed disease, if PSTV is found and confirmed by an inspector, the infected plants must be isolated and disposed of. The farm must undergo thorough disinfection. In addition, the Act requires the planting of Certified or better grade seed for commercial plantings, which further prevents buildup of PSTV and PVX in tablestock or in crops grown for processing purposes.

In New Brunswick, samples from all fields grown for seed of grades Foundation and above are required by law to be grown in Florida during the winter for disease readings. Similarly, the 1986 amendment of the Prince Edward Island Plant Disease Eradication Act of 1974 requires that any person growing more than 0.1 hectares of potatoes must plant "Certified" or a better class of seed potatoes. Planting of botanical seed is permitted only if the seed is certified by an agency in Canada (6).

I. **Private company's co-operation.** In an effort to minimize the buildup of pathogens by the repeated planting of seeds, the major potato processing company in New Brunswick made it compulsory for their contract growers to plant Foundation class seed for processing purposes (3).

J. **Tissue Culture Plant Propagation Centres.** The purpose of most of the Plant Propagation Centres established throughout Canada is to provide potato plantlets of high quality to the potato industry of that province. Tested tubers with no detectable potato diseases are greensprouted in a growth cabinet. These sprouted tubers are surface sterilized in a solution of commercial bleach and rinsed in sterile, distilled water. Using sterile culture procedures, small portions of the growing tip, less than 1 mm in length, are removed and placed in a test tube containing a liquid nutrient medium and growth hormones. The tip develops slowly over the next few weeks, and then is transferred to a new tube containing a nutrient medium, without growth hormones, where it continues to grow and develop. When the plantlet produces roots and has filled the entire test tube, it is cut into microcuttings comprised of a leaf, axillary bud and stem segment. Each segment is capable of producing a new test tube plantlet within 3-6 weeks. These plantlets are grown into mature potato plants in the greenhouse at the Elite seed farms or transplanted directly to the field and monitored for diseases. Greenhouse tubers or transplanted plantlets are planted in the field to give the first pre-Elite generation. At present, depending on the province, 50-70% of pre-Elite seed is derived from these plant propagation centres.

K. **Monitoring of diseases by seed certification laboratories.** In most of the seed potato-producing provinces in Canada, personnel trained in the latest methods of diagnosis operate well-equipped laboratories called potato seed certification laboratories. Their main function is to monitor tissue culture plantlets, greenhouse-grown tubers, materials from seed farms grown in the field, and also to monitor the disease status during the growing season. Thus, PSTV and latent viruses missed at one stage could be detected at a later stage and, in this way, kept out of the seed producton system.

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CONTROL OF MYCOPLASMA DISEASES

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ABSTRACT

Yellows diseases, caused by mycoplasma infections, affect wide ranges of plants, both dicotyledonous and monocotyledonous species. Some yellows agents infect potato in the field or can be transmitted to potato experimentally. However, disease symptoms in the inoculated potato are not of diagnostic value except to distinguish two major groups of mycoplasma diseases, namely the aster yellows and the witches' broom. Neither of these diseases is contact-transmissible nor true-seed-borne. The yellows agents depend on leafhoppers for transmission, and disease spread in the field is affected by leafhoppers that carry the yellows agents originating from weeds or other crops in the surrounding areas. Transmission of the yellows agents does not occur directly from mycoplasma-infected potato. Symptom development may be arrested by antibiotics of the tetracycline group, and individual infected plants may be cured by heat therapy. For disease diagnosis, direct proof of pathogenicity is required by Koch's postulates but it has not been established with these yellows diseases, thus the disease agents are called mycoplasma-like organisms (MLO). The best evidence of the association of MLO with yellows diseases is the electron microscopic observation of MLO and the demonstration of their serological identity. More sensitive and accurate methods of differentiating between MLO pathogens are urgently needed. Overall control measures are discussed with reference to the Canada seed potato certification scheme.

RESUME

La jaunisse, causée par les mycoplasmes, affecte plusieurs espèces' de plantes monocotyledones et dicotyledones. Plusieurs variétés de mycoplasmes infectent les plants de pommes de terre dans le champs, ou les tubercules directement dans le laboratoire. Cependant, les symptômes des maladies n'ont aucune valeur diagnostique si ce n'est que pour distinguer deux groupes de maladie, la jaunisse de l'aster et le balai de sorciere qui ne se transmettent ni par le contact et ni par les semences. L'agent principal vecteur de la maladie est une sauierelle qui transporte les mycoplasmes originaires des mauvaises herbes ou des cultures a travers une région donnée. La transmission des mycoplasmes ne se fait pas directement par les plants ou les tubercules infectés. Le developpement des symptômes peut etre arrete par les antibiotiques de la famille des tetracyclines. Le diagnostique de la maladie, qui demande une preuve directe de la pathogenicité par le postulat de Koch, na' pas été établie dans le cas des maladies causeés pas les mycoplasmes. Comme resultat, les agents causant la maladie sont referés comme étant des organismes de type mycoplasmes (OTM). L'evidence la plus sûre pour verifier l'association des OTM avec la jaunisse est obtenue par le microscope électronique et par la demonstration d'une identité commune suivant des méthodes sérologiques. On a besoin de methodes plus sensibles et précises pour differencier

entre les pathogenes OTM. Les mesures de contrôle avec references à la certification de la semence des pomme de terre au Canada sont discuteés.

INTRODUCTION

Mycoplasmas (class, Mollicutes; order, Mycoplasmatales) are considered to be the causal agents of yellows diseases of plants, formerly thought to be of viral origin because of close resemblance in symptomatology and mode of transmission. In plant pathology, however, since the initial discovery in 1967 (8), the term "mycoplasma-like organisms (MLO)" has been in use to describe a group of procaryotic microorganisms that morphologically resemble members of the Mycoplasmatales but lack a proof of Koch's postulates. Most attempts to isolate and culture these microorganisms, except those belonging to the genus *Spiroplasma* (40), have been in vain. MLO have been found in more than 200 plant species and in a large number of arthropods, which, in many cases, serve as very effective vectors. In order to formulate effective control measures for any plant disease, it is essential that the disease-causing agent is correctly identified, the vector and its behaviour are properly understood, and disease characteristics fully recognized. Furthermore, it is important to utilize highly sensitive diagnostic tools for the detection of the disease-causing agent. All these areas will be briefly described for MLO and MLO diseases of potato (*Solanum tuberosum* L.) in conjunction with the discussion of control of MLO diseases of potato.

MLO DISEASES OF POTATO

The potato diseases associated with MLO occur worldwide (2, 8, 10, 12, 16, 25, 42, 43) and they have been described under various names in different parts of the world; for example stolbur (39), parastolbur (38) and metastolbur (36, 37) in Europe, tomato big bud in Australia (12), purple top-roll in India (26). In the western hemisphere, aster yellows of potato has been variously referred to as purple-top wilt (43), yellow top, bunch top, purple dwarf, apical leaf roll, and hay wire (30). However, one must recognize that the use of symptoms to differentiate MLO is not reliable. Under field conditions, symptom production may be influenced by the potato cultivar affected, the time of infection, environmental factors and other conditions. Future investigations may clarify whether these diseases are caused by distinct MLO or are caused by the same MLO or by different strains of the same agent. Brief descriptions of two major MLO diseases recognized in North America are given in the following.

SYMPTOMS

Aster yellows (purple-top wilt). Aster yellows is one of the most widespread diseases of plants. Some 300 species of crop and weed plants in 48 families (3 monocots; 45 dicots) are susceptible. In potato, it is not tuber-transmitted and the symptoms do not develop on young plants, but the first symptoms appear at or after blossoming. The infected plants always wilt two or three weeks after the development of initial symptoms. There is usually necrosis of the vascular elements at the base of the stem, often spreading to the stem end of the tubers.

Young leaflets roll and develop purple or yellow pigmentation after infection. Infected plants commonly form aerial tubers and, occasionally, proliferation of axillary buds can be seen. Plants are often stunted and severely affected plants may die prematurely. All potato cultivars in Canada are suceptible and sometimes severe losses occur (17). The severity of the symptoms, including the purple pigmentation and production of aerial tubers, may vary with the potato cultivars, light intensity, temperature, and many other factors (21).

Witches' broom. Infected plants produce many axillary and basal branches with simple, small "round" leaves, which may be chlorotic. Symptoms after infection in the current season appear late, if at all, and consist of an upright habit of growth, rolling of leaflets and some discoloration in apical leaves. MLO of witches' broom are tuber-perpetuated, in contrast to those of aster yellows (21). Affected hills may produce tubers that appear normal during the year of infection but give rise to plants with severe symptoms in the subsequent year. Tubers from infected plants often lose dormancy and frequently produce hairy sprouts. When planted, they produce many small tubers and an increased number of sprouts with simplified, small leaves (42, 48).

CAUSAL AGENT

The MLO found in plants and vector insects are morphologically similar to genuine mycoplasma (25). MLO bodies are bounded by a unit membrane and contain ribosome-like osmiophilic particles and fibrillar DNA-like material in the central core area (8). MLO are pleomorphic and form spherical (60 - 100 nm diameter), globular (150 - 1100 nm diameter) and filamentous bodies often accompanying intermediate forms or branching or 'budding' forms (25). The MLO change morphologically during the course of disease development and depending on cellular environment. Filamentous bodies have been observed in the proximity of sieve pores in the sieve tubes, some of them passing through the sieve pores (8, 19, 25). Small bodies with condensed osmiophilic material are considered the degenerative product probably resulting from nutritional deficiencies and unfavorable physiological changes of the affected host cells.

PATHOGENICITY

The detection of MLO in plants, their intracellular multiplication in infected tissue and their transmission by insect vectors from diseased to healthy plants is not direct proof of MLO pathogenicity. Direct proof of pathogenicity must satisfy Koch's postulates. Thus far, these postulates have been fulfilled with isolates of spiroplasmas (40), but not with MLO.

Circumstantial evidence suggesting MLO as disease-causing agents is their constant association with diseased but not healthy plants, their adverse effects on invaded and surrounding plant cells, disease development following insect vector, dodder (*Cuscuta* spp.) and graft transmission, symptom remission and the disappearance of MLO from plants after treatment with tetracycline antibiotics and the therapeutic effect of heat treatment on the diseased plants and insects (25).

MODE OF TRANSMISSION

The transmission of MLO from plant to plant is, in general, dependent on insect vectors (17, 21, 25, 28, 43). Transmission by grafting and the parasitic plant *Cuscuta* have been demonstrated. Although grafting is normally restricted to closely related plants, it has been shown that the implantation of diseased plant tissue onto unrelated indicator plants can result in transmission in some cases. A number of species of *Cuscuta* have been shown to act as a plasmatic bridge for MLO and have been used for experimental transmission of MLO. The MLO can multiply in the *Cuscuta* tissue and may also develop disease symptoms.

EPIDEMIOLOGY

The leafhopper vector of aster yellows, *Macrosteles fascifrons Stål*, overwinters in the egg stage on weeds, grasses, and small grains. MLO-infected leafhoppers may be carried a thousand miles or more in the spring and early summer and be distributed over wide geographical areas. MLO must multiply within both nymphs and adult leafhoppers, usually for 9 to 16 days after being acquired by the leafhoppers. After this incubation period that is partially influenced by temperature, these insects are capable of transmitting MLO. The adult insect continues to transmit MLO as long as it lives (average, about 65 days).

The MLO also has an incubation period in the host plant that ranges from 9 to 40 days or longer, depending on the age and vigor of the plant, and temperature. In potato, the incubation period after transmission by leafhopper is 34 to 68, average 49, days and is longer than in asters and some other plants (21).

Disease incidence is influenced not only by a population of the MLO-carrying vector in the field, but also by the relative abundance and kind of MLO reservoir, temperature, and other climatic conditions affecting MLO, host, and vector.

In the potato field, neither nymphs nor adults can acquire the MLO from potato (21). Transmission of aster yellows MLO to potato occurs only when the leafhopper has fed on some other infected host species two to three weeks before feeding on potato. This is also true with witches'-broom (28). Witches'-broom in perennial legumes such as clover is usually more serious than in potato because the former is a preferred host by the vector, and inoculum sources are usually available within or around the crop. Witches'-broom MLO are transmitted by leafhopper vectors, *Scleroracus flavopictus* Ish. (*Ophiola flavopicta* Ish.), *S. balli* Med. and *S. dasidus* Med. (10, 28).

HISTOPATHOLOGY

MLO are generally confined to the sieve elements of the phloem (8, 9). They have occasionally been observed in the parenchyma and companion cells of the phloem and, in some cases in the cortical parenchymatous tissues. The purple-top wilt of potato, which is caused by aster yellows MLO, induces necrosis of phloem and later also of adjacent parenchyma (21). The cambium may show a disturbance of the normal orderly arrangement of cells (14). Sometimes, the phloem parenchyma cells show hypertrophy and collapse of cells. The fiber initials may collapse. An abnormal production of secondary phloem cells may be pronounced. Abnormally excessive amounts of callose, which can be detected by aniline blue staining, occur in the affected sieve tubes (13, 14, 15). The hyperplastic tissue, particularly that of the primary phloem, often collapses and secondary hypertrophy and hyperplasia may follow.

Hyperplasia with production of abnormally numerous sieve-tube elements occurs in the external and internal primary phloem, in the secondary phloem and even in the parenchyma outside but adjacent to the phloem (14). The secondary phloem usually shows less collapse and necrosis, and a more orderly cell pattern than the primary (14). The histopathological information of MLO infected plants is valuable in understanding disease processes and interpretation of diagnostic anatomical data.

METHODS OF DIAGNOSIS

Diagnosis for potato MLO diseases may be divided into 1) microscopic methods, 2) serological methods, 3) biological methods and 4) chemical methods.

1. Microscopic methods

Electron microscopy. The most important and widely accepted diagnostic procedure is electron microscopy (8, 14, 25). Its main advantage is that observation of basic morphology of MLO in a yellows-diseased plant gives definitive evidence for the association of the MLO with the disease. However, negative results are often misleading since only a small area of the diseased tissue is examined by electron microscopy at high magnifications and the distribution of MLO in the yellows diseased plants is known to be irregular. Another consideration that is important for detection of MLO is the choice of host plant. When a host that responds with acute necrosis to MLO infection is used, the examination by electron microscopy can be negative (22). Negative staining methods of plant extracts have been tested. However, they were not specific enough to be useful for MLO diagnosis. Similar spherical bodies observed in both diseased and healthy plant tissues were considered to be artifacts (41).

MLO can be detected by immunosorbent electron microscopy (ISEM) in partially purified preparations (33). Although ISEM appears to be less sensitive than enzyme-linked immunosorbent assay (ELISA), it has an advantage that the diverse morphological features of the MLO can be seen in positive serological reactions. The use of immuno-gold labeling may improve the sensitivity of MLO detection by ISEM.

Light Microscopy. Light microscopy used with or without different staining techniques has been applied to yellows-diseased plant tissue and could be of significant practical value in diagnosis, although the techniques are not specific enough to distinguish between different MLO.

Ultrathin sections embedded in epoxy resin can be stained with toluidine blue. Differences in the intensity of staining can be detected in the area of phloem element invaded by MLO. This technique also accelerates selection of the phloem elements which have been invaded by MLO for further electron microscopy. Histochemical techniques, such as staining with Feulgen stain (20), methylene green- pyronine or Dienes' stain (7) have also been used to demonstrate the presence of MLO.

Different fluorochromatic techniques in combination with the UV light microscope have proved to be effective diagnostic tools. A positive correlation between callose formation and degeneration processes in diseased phloem tissue due to MLO infection can be demonstrated by staining a section with water-soluble aniline blue (13, 14, 15). Improved results have been reported by treating glutaraldehyde fixed tissue with polyethyleneglycol 4000 and staining with Azur I, or fast green (11). The demonstration of MLO-DNA in the infected tissue by staining with DAPI (4'-6-diamidino-2-phenylindole.2HCl), a DNA-binding benzimidole derivative, and with other less specific cytochemical fluorescence techniques has been found useful for the diagnosis of MLO diseases (3, 13, 16, 29). Certain modifications of the DAPI procedure have been suggested in an attempt to increase its sensitivity, such as combined use of berberinesulfate (27) and the pretreatment of sections with pectinase to induce phloem tissue separation prior to DAPI staining (3). DAPI also reacts with DNA-viruses and with DNA-containing cellular organelles under certain conditions.

2. Serological methods

Attempts to produce specific antibodies to partially purified MLO antigens have been made by different MLO research groups (4, 5, 24, 31, 32, 33). The titres of antiserum produced against partially purified plant MLO antigens are rather low (1/8 - 1/16) and the antiserum preparations also contain antibodies to host components, which must be removed prior to diagnostic use. Polyclonal antibodies from rabbits were used in double diffusion tests (31), ELISA (4, 31), immunosorbent electron microscopy (33) and indirect immunofluorescence microscopy (5). Monoclonal antibodies to MLO produced in mice were used in ELISA and direct immunofluorescence microscopy (23, 24). It was possible to distinguish differences between different MLO preparations by the use of monoclonal antibodies (23).

3. Biological Methods

Although it is not direct proof of MLO etiology, the pathogenicity of MLO in sap extracted from diseased plants can be demonstrated by individually injecting a small amount of fresh sap preparations into leafhoppers of a known vector species, which are then reared on suitable test plants for symptom development.

4. Chemical Methods

Antibiotics treatment. The remission of symptoms was observed after treating different MLO diseases, including aster yellows and witches' broom, with tetracyclines (6, 18) Since MLO are highly sensitive to tetracyclines, this is one of the most basic and simple methods of determining the presence of MLO. In most cases, some tuber formation was initiated within one month after administration of the antibiotic. These newly initiated tubers could be sprouted, and resulted in healthy growth. However, when removed from the tetracycline, haywire symptoms recurred in 50% of the potato plants within 30 days (30).

Histochemical staining. Dienes' stain, a specific stain for animal mycoplasmas reacts with MLO within sieve tubes of infected plants (7). The technique is rapid and simple, and requires only inexpensive reagents and laboratory equipment.

Specific DNA hybridization. Specific DNA probes are useful for assaying medical mycoplasmas (34). Probes made by nick translation of total cell DNA of three spiroplasmas (corn stunt spiroplasma, *Spiroplasma citri*, and BC3) were used in detecting their respective spiroplasma infections within leaf hoppers by the dot blot hybridization methods (1). With further refinement, the method will be useful for detecting MLO infections.

CONTROL

The discussion of control measures can be divided into four phases of operation.

Phase one consists of intensive tests of pre Elite materials by applying available MLO detection methodology. Tissue culture may be effective in eliminating MLO under certain culture conditions (35). Since there are no visible symptoms developed at early stages of MLO infection, careful tests using highly sensitive techniques are essential at this stage of operation. Phase two covers the period of field multiplication of selected Elite I, II, and III materials. Potatoes certified in Elite I and II classes are the basic stocks used to produce all seed in the commercial classes Elite III, Foundation and Certified. For this purpose selection of isolated fields, as far away as possible from clover fields, is recommended. Weeds, in particular clovers, are known to be a perennial source of MLO, thus good weed control is essential. If plants showing any MLO symptoms are found, they must be rogued out immediately. Suspect plant materials may be tested for MLO if only a limited amount of seed material is available; otherwise, stringent roguing must be applied. The natural spread of MLO diseases can be controlled in most cases with insecticides. Since there is no transmission of MLO between potato plants, insecticide sprays must be directed to weeds around potato fields, if spraying is deemed necessary. Phase three covers the period of Foundation and Certified seed production. Control practices are essentially the same as those for phase two. However, because of larger areas for seed potato production than for the preceding classes, intensive testing may not be practical. Rigorous eradication of diseased plants, if found, must be continued to reduce the source of new infections to conform with the existing seed potato certification scheme. The production and use of certified seed ensures the maintenance of high yielding and high quality commercial potato production. Phase four is focused to breeding for resistance. This is a long-term project that aims at protection of potato crops from heavy losses by incorporating resistant genes from different sources, which may result in the development of new cultivars. This is probably the only effective and practical solution to be attained.

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ROLE OF PLANT QUARANTINE IN PEST CONTROL

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ABSTRACT

Agriculture Canada's Plant Health Division administers the Plant Quarantine Act (1968-69) which protects Canada's agricultural industry from the introduction of plant pests. Specifically, it provides powers to exclude non-indigenous pests, to prevent the spread of pests that are subject to domestic quarantine, to control the movement of plant pests from one part of the country to another, and to conduct eradication. Furthermore, it is responsible for upholding Canada's commitment to the International Plant Protection Convention (1951) which entails certifying that exports from Canada meet the phytosanitary requirements of importing countries.

RESUME

Le Service de la Sante des Plantes d'Agriculture Canada administre l'Acte pour la mise en Quarantaine des plantes (1968-69) qui protege l'industrie agricole contre l'introduction des parasites des plantes. Plus specifiquement, l'Acte fourni les pouvoirs d'exclusion des parasites non-indigenes, de prevention de la dispersion des parasites sujets a une mise en quarantaine domestique, de controle du mouvement des parasites des plantes d'une region du pays a une autre, et d'eradication. La Division se doit aussi d'assurer que le Canada respecte la Convention Internationale pour la Protection des Plantes (1971) en certifiant que les exportations canadiennes rencontrent les exigences phytosanitaires des pays importateurs.

INTRODUCTION

The Plant Health Division of Agriculture Canada is responsible for administering Canada's Plant Quarantine Act of 1968-69(1). This provides the Division with authority to achieve four broad objectives with respect to the control of pests of crop production in Canada:

1. Exclude plant pests (insects, nematodes, fungi, bacteria, viruses, mycoplasmas, etc.) that are either not already present, or that if present, are being actively eradicated.

2. Prevent the spread of pests that are present, but the distribution of which is limited.

3. Eradicate or suppress pests of local distribution when their economic significance warrants it (from a production and marketing standpoint).

4. Ensure that products moving within or from Canada are free from pests of concern to the receiving region or country.

In the case of potato (*Solanum tuberosum* L.), a crop of major economic significance to Canada, the Plant Health Division has active programs in all four areas.

EXCLUSION

Despite many years of unregulated movement of agricultural products prior to the beginning of this century, Canada is still free from a number of potato pests of significance (Table 1). Pests not present are therefore prohibited from entry.

Table 1. Potato Pests of Quarantine Significance Not Present in Canada

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VIRUSES

Andean potato latent virus (APLV)
Andean potato mottle virus (APMV)
Aracacha virus B (AVB)
Potato mop top virus (PMTV)
Potato virus T (PVT)
Potato virus V (PVV)

Potato calico strain of tobacco ringspot virus (TRSV-ca)
Tobacco necrosis strain of potato virus Y (PVY-n)
Resistance breaking strain of potato virus X (PVX-hb)

BACTERIA

Brown rot (*Pseudomonas solanacearum* E.F. Smith)

FUNGI

Common rust (*Puccinia pitteriana* P. Henn.)
Deforming rust (*Aecidium cantense* Pers. ex Pers.)
Gangrene (*Phoma exigua* Desm var *foveata* [Foister] Boerema)
Thecaphora smut (*Angiosorus solani* [Barrus] Thirum. & O'Brien)

INSECTS

Potato tuber moth (*Phthorimaea operculella* Zeller)

NEMATODES

Columbia root knot nematode (*Meloidogyne chitwoodi* Golden, O'Bannon, Santo and Finley)

In addition, there are also other pests, e.g., two species of the potato cyst nematode (Glodobera rostochiensis [Wollenweber] Behrens, and G. pallida [Stone] Mulvey and Stone) and potato wart (Synchytrium endobioticum [Schilb.] Perc.), that although they are present in Canada, are currently restricted to localized pockets in two geographically isolated areas (Vancouver Island having just G. rostochiensis and Newfoundland having all three). Potato production areas on the mainland are thus free of these pests and must be protected from their introduction from domestic and international sources.

The net effect of these restrictions is that, at the present time, importation of seed potatoes is permitted only from certain areas of the United States, and only then if the risks are considered acceptable both to federal certification officials and provincial officials (where they have jurisdiction). Introduction of potato germplasm from outside North America is only possible if it enters through a post-entry quarantine facility. The Plant Health Division presently operates such a facility in Ottawa.

Post-Entry Quarantine

Current rules permit potato germplasm to enter Canada in one of three forms: tuber, in vitro plantlet, and true seed. The preferred form is the in vitro plantlet as this will be free from a number of diseases that are restricted to the tuber. If it is necessary to import the other propagule types, then these are transferred into culture as soon as possible after arrival. The policy is thus to hold imported germplasm in a culture bank while it is in quarantine and to withdraw plantlets from this bank for planting in the greenhouse and testing.

Table 2. Methods for detecting viruses in quarantine material

Indigenous viruses		Non-indigenous viruses	
PLRV	S	APLV	S*,I
PVA	S,I	APMV	S*,I
PVM	S,I	AVB	S*,I
PVS	S,I	PMTV	I
PVX	S,I	PVT	S*,I
PVY	S,I	PVV	S*,I
TRV	I	PVX-hb	S, I
PSTV	D	PVY-n	S, I
		TRSV-ca	S*,I

Legend S= serology, I=bioassay on indicator hosts
D= Dot-blot cDNA assay, *=projected

Methods being used for virus diagnosis are shown in Table 2. As is indicated, antisera are not yet in use for most of the non-indigenous viruses, but it is anticipated that these will be available in the next few years. The serological test in current use is ELISA (2). Plants are also visually assessed for possible virus symptoms, and sap extractions are screened in an electron microscope for virus-like particles. Bacterial ring rot (Corynebacterium sepedonicum [Spieck. & Kott.] Skapt. & Burkh.) is tested for using serology (latex agglutination [6], and immunofluorescence [3]) and culture on Richardson's medium (5).

PREVENTION OF SPREAD

The potato cyst nematode and wart disease are the two potato pests that are regulated to prevent their movement within Canada.

On Newfoundland where both pests exist, there is a strict quarantine against the movement of both potatoes and soil to the mainland. The restriction on soil can also have the effect of prohibiting the movement of root crops such as rutabaga. Soil is removed from all vehicles leaving that island by subjecting them to inspection and passing them through a car-wash.

On Vancouver Island, there is a similar restriction on the movement of soil from the quarantine zone and a prohibition on growing hosts of the potato cyst nematode, i.e., potato, tomato, and eggplant.

ERADICATION

In addition to attempting to prevent the spread of the cyst nematode and potato wart beyond their present ranges, the long term objective of the Department is to eradicate these pests. Among the current measures in effect are that new varieties can only be registered for production in Newfoundland if they have immunity and high levels of resistance to, respectively, potato wart and the golden nematode. On Vancouver Island, production of potato and other hosts (e.g., tomato and eggplant) is prohibited in the quarantine zone.

Efforts to eradicate ring rot disease are presently restricted to the imposition of a zero tolerance in the Seed's Regulations and the exercise of provincial authority (in some provinces) as to what is imported, what is planted (Certified or better), and what assistance is provided for "clean-up". Considerable testing is also underway in some provinces to identify sources of infection.

With respect to spindle tuber disease, it is believed that, as a result of applying a zero tolerance in the certification program (with the assistance of testing, and operating a "flush-through" system), this disease has now been eradicated. However, this can only be proven by conducting surveys; such a program is now underway.

EXPORT CERTIFICATION

Canada is a signatory to the United Nations Food and Agriculture Organization International Plant Protection Convention of 1951 (4). As such, the Plant Health Division is responsible for the issuance of certificates relating to the phytosanitary condition and origin of consignments of plants and plant products moving in international trade in order to comply with the requirements of importing countries; it is also responsible for reporting the outbreak and spread of important pests.

Because phytosanitary certificates often state requirements that exceed Canada's normal requirements for seed certification, export certification can have a major impact on the pest control practices that producers need to follow if they are interested in exporting. For example, a number of countries have very low tolerances for scab (*Steptomyces scabies* [Thaxter] Waxman & Henrici) and black scurf (*Rhizoctonia solani* Kuhn) diseases. Meeting these tolerances often requires the use of special management practices.

Probably the biggest impact of export certification, however, has been the pressure it has created to eradicate ring rot and spindle tuber diseases. Although Canada has zero tolerances for these diseases, the derogation terms that permit Canada to export into the member countries of the European Economic Community impose severe regulatory restrictions that make almost any incidence of these diseases very difficult to live with.

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WEED CONTROL RESEARCH IN POTATOES IN CANADA

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ABSTRACT

Canadian literature on weed research in the potato crop in Canada was reviewed, current research directions and person year inputs determined, and future needs and direction discussed as a base for discussions during the symposium. Research on control of annual broadleaf and annual grass weeds has provided an excellent array of herbicides that will provide control of these on the potato crop. New research is providing postemergence herbicides that will give control of quackgrass, however, research has not given success on control of perennial broadleaf weeds. Likewise, limited research has been conducted on weed interference, weed biology and chemical interactions which will provide data that are necessary for development of integrated weed management practices for the potato crop. Current person year input in weed research in the potato crop is 1.53 p.y. nationally, with approximately 90% of this devoted to herbicide evaluation and use pattern determination. No change is expected in the future with current low levels of support and cuts at all levels of research. A number of research priorities are presented but increased resources and a national coordinated plan will be necessary if major advances are to be made in the future for weed control and integrated weed management in the potato crop.

RESUME

La littérature canadienne portant sur la recherche contre les mauvaises herbes en culture de pomme de terre a été revue, les orientations de recherche et les ressources humaines établies, et les besoins et l'orientation future discutée afin d'établier une base pour la discussion générale lors du Symposium. La recherche sur le contrôle des plantes annuelles à feuilles larges et des graminées annuelles a produit un excellent inventaire d'herbicides pour leur contrôle en culture de pomme de terre. La recherche en cours est en train de nous donner des herbicides de post-émergence qui contôleront le chiendent. Les résultats sont moins encourageants pour les plantes vivaces à feuilles larges. Relativement peu de recherche a été faite sur l'interférence par les mauvaises herbes, la biologie des mauvaises herbes et les intéractions entre produits chimiques. Ces connaissances sont cependant nécessaires au développement des pratiques de gérance intégrée des mauvaises herbes en culture de pomme de terre. A l'échelle nationale, 1.53 personne-année est dédiée à la recherche sur les mauvaises herbes en culture de pomme de terre. Environ 90% de ces ressources vont à l'évaluation des herbicides et de leur mode d'utilisation. Aucun changement n'est anticipé si l'on considère le faible niveau de support actuel et les coupures générales en recherche. Un nombre de priorités de recherche sont présentées mais elles requièrent des ressources accrues et un plan de coordination nationale si l'on espère d'importants développements dans le domaine du contrôle et de la gérance intégrée des mauvaises herbes en culture de la pomme de terre.

INTRODUCTION

This symposium was organized to review the state of knowledge in all the facets of crop protection of potatoes in Canada. We were asked to prepare a background paper on weed science research in Canada that would (a) provide an overview of the situation as it now exists based on the literature published from Canadian sources, (b) look at the resource input at present into weed research in Canada, and (c) give some thought to the areas that must be addressed in the future to gather the knowledge that will be necessary before we will be able to put into place an integrated weed management system for potatoes that minimizes the use of herbicides. We have attempted to do this while, at the same time, raising as many questions as possible that will hopefully stimulate discussion. Readers are referred to a review paper (5) for information on weed control methods in potatoes in the United States up to 1971.

REVIEW OF LITERATURE

WEED CONTROL WITH HERBICIDES

Control of weeds in the potato crop has traditionally depended on the use of cultural and mechanical practices. As a row crop, the potato is well suited to this type of program as it must be cultivated to cover the crop in the row to prevent greening. Because of the delay in emergence of crop relative to the weeds, a light harrowing at crop emergence has traditionally been used to control the small emerged annual broadleaf weeds. Subsequent cultivation and hilling kept these weeds under control for the early part of the growing season. Control of annual grasses, such as barnyard grass, by this method was not as successful however, as emergence of these warm season plants is often later after the first hilling and the plants were not controlled or were shifted to the row where they caused more problems to the growing potato crop. Control of perennial grasses likewise was not adequate, especially when the population was at a moderate or greater level. In a recent paper, the advance of weed control technology in the Atlantic Region was reviewed (7) and it was noted that growers now rely on herbicides to give season-long weed control. The author traced the development of dinoseb from 1946 and the addition of the several herbicides which are now the standard herbicides recommended in the production guides of Canada.

Weed control in the potato crop has progressed to a level at which there are now a number of safe and effective herbicides available for use by growers. Current recommendations in the Canadian Potato Guides now number 10 separate herbicides which can be used alone or in combination with others (Table 1). The spectrum of weeds controlled is broad and herbicides are available to control annual broadleaf weeds, annual grasses, and quackgrass. Control of the common broadleaf weeds is excellent with herbicides such as paraquat, metribuzin, linuron, metobromuron, monolinuron, and prometryne. Annual grass control can be accomplished with the preemergence products metolachlor and metribuzin, dalapon applied at ground crack, and also with the postemergence products such as diclofop-methyl and sethoxydim. Quackgrass control is possible by integrating into the production system the use of glyphosate, the use of paraquat as an at-ground-crack treatment on emerged grass, or by use of the postemergence in-crop herbicide sethoxydim. The grower has the possibility of using a single herbicide to control one type of weed problem or he can use a program of herbicides to control several types of weed problems that he knows are present in his production fields.

Table 1. Herbicides presently recommended in Provincial Weed Control Guides.

Timing	Herbicide	Weeds Controlled
Preplow	glyphosate	emerged perennials and annuals
	dalapon	emerged grasses
Preplant	EPTC	annual broadleaf and grasses partial control of quackgrass
	metribuzin	annual broadleaf and grasses
Preemergence	linuron	annual broadleaf
	metribuzin	annual broadleaf and grasses
	metolachlor	annual grasses
	metrobromuron	annual broadleaf and grasses
	monolinuron	annual broadleaf
	prometryne	annual broadleaf
Ground crack	paraquat	emerged weeds
	dalapon	quackgrass
Post-emergence	diclofop-methyl	annual grasses
	sethoxydim	annual grasses and quackgrass
	metribuzin	annual broadleaf and grasses
	EPTC	annual broadleaf and grasses

One area of weed control, however, is not as well advanced as the others and this is the problem of control of the perennial broadleaf weeds such as field mint, narrow-leaf goldenrod, perennial sow-thistle and Canada thistle. All of these plants tend to be at the young shoot stage of growth when the potatoes are emerging and, because of their extensive underground root and rhizome system, are not controlled by applied herbicides. There may be a burn-off of emerged shoots but the plant soon regrows and provides significant interference with the potato crop. Some control can be achieved by the use of glyphosate integrated into the rotation but even this is not the best solution, as best control of these broadleaf perennials requires application at the flowering stage in most cases. This necessitates that the field be fallowed for a year to have the weed at the best stage for application. This is not a practical solution. Patches in the field can be controlled by application of the non-selective herbicides but this will result in kill of the crop in the area treated and will result in a loss to the grower. As a result, this type of application is not often used in potato production because of the high dollar investment in the crop and the chance of contamination of the remaining crop with the non-selective herbicide.

CULTIVAR TOLERANCE

The herbicide paraquat has been used in P.E.I. for a number of years as an inexpensive herbicide to control emerged weeds when applied at the ground crack stage of potato growth. Level of crop injury is dependent on rate and time of application and also on the cultivar grown. Work has shown that delayed application of paraquat on Kennebec and Sebago cultivars resulted in reduced yields of Sebago if application was made when emerged shoots had reached 7.5 cm in height (12, 13). Development of the new selective herbicide metribuzin for potatoes gave in a new level of control of weeds in the crop as spectrum of control was broadened and control of annual grasses and broadleaf weeds was accomplished with one herbicide. This herbicide, however, also had the problem of differential cultivar tolerance as some of the cultivars were susceptible to the herbicide.

Problems were noted in grower fields and researchers were quick to determine that some cultivars were susceptible, depending on the stage of application and rate of application. Several researchers evaluated numerous cultivars and susceptible cultivars were identified (4, 10, 11, 14, 21, 24). Additionally, the genetics of the transfer of the susceptibility was determined to be due to a single recessive gene (6).

INTERFERENCE FROM WEEDS

All weeds are known to interfere with the growth of the crop and cause a loss of yield and often a reduction in quality. The weeds compete with the crop for available light, space, nutrients and water. The degree of loss of crop yield will be dependent on the aggressiveness of the crop and weed and the density of the weeds/unit area. Also of concern is the time at which the interference occurs and the type of weed, such as annual broadleaf vs annual grass or annual vs perennial weed. In the potato crop, researchers have been concerned mostly with the control of weeds so as to maximize yield and, as a result, have neglected the study of the effect of weed interference, either as a complex of weeds or as individual species, on the crop.

A review of the literature on weeds and potatoes showed that little data is available from studies in Canada but one study in Quebec with Norland and Kennebec showed that hilling at potato emergence gave best weed control and later hilling required a herbicide for best results (25). Time of hilling had more effect on vegetative growth of the potato than on level of weed control. A study from North Dakota on the effect of a mixed stand of annual broadleaf and grass weeds showed that weeds emerging one week after and competing all season with potatoes (Norchip and Viking) reduced tuber yield 54% compared to 16% when weeds emerged 3 weeks after potatoes (20). The weeds reduced both size and numbers of tubers and, in some cases, reduced the percentage of marketable tubers. The effect of quackgrass interference on Russet Burbank yield was studied and it was found that delaying the removal of a pure stand of quackgrass for 2 weeks after potato emergence reduced small, marketable and total yield by 6, 27 and 21%, respectively (18). Longer delays in removal of the weed gave greater yield losses. Degree of yield reduction was dependent on level of infestation, with a population of 50 shoots/square meter reducing yields much less than a heavy population of close to 200 shoots/square meter. In another study, it was reported that delaying application of sethoxydim to a 150 shoot/square meter population of quackgrass at the 6 leaf stage instead of at the 3-4 leaf stage resulted in yield loss due to early quackgrass interference (17). No other studies on weed interference were found in literature but, in a related field of study, it was noted that potato cultivars that emerged quickly, had early rapid growth, and maintained a dense leaf canopy throughout the growing season, were better able to compete with weeds (30).

WEED BIOLOGY

Weed scientists have also tended to neglect the study of the weed problem itself so that there is little data available on the growth and development of weed species that would be useful in the development of integrated weed control systems for the potato crop. This is not surprising, however, as the major concern was the development of effective control measures and the new herbicides which have become available since the end of the Second World War made this possible. Some of the annual weeds, such as the more common broadleaf species and annual grasses, have been studied in other cultivated row crops and inferences can be drawn from these studies for use in the potato crop, but data is still needed on the growth of the weeds in the potato crop to be able to develop weed management packages. Little data is available on the biology of the perennial grass, quackgrass, as it relates to potatoes even though it is a major problem in the potato crop. With the effective control of the annual broadleaf and grass weeds with herbicides, the perennial broadleaf weeds have become more of a problem, yet the biology of these weeds and their relationship to the potato crop has not been studied. As control of annual weeds becomes more assured with good herbicides, the detrimental effect of perennial grass and broadleaf weeds becomes more apparent and more research is needed on these individual species in the potato crop.

HERBICIDE RESIDUES

Many of the herbicides used in the potato crop are persistent in soil and may carry over to the next year to damage crops grown in rotation. Likewise, many herbicides used in other crops may persist to damage potatoes grown in rotation. Little data is available on these problems as they relate to the potato crop but some studies have been conducted on a few of the herbicides used. Chlorbromuron, used for weed control in potatoes, was shown to remain in the top 2.5 cm of soil and residues in the soil dropped to 25% of that applied by the end of the growing season (23). Metribuzin applied to potatoes as a preemergence treatment was shown to have a half-life of 30 to 39 days in a fine sandy loam soil on P.E.I. (16). Residues from an application of up to 1.5 kg ai/ha had no effect on yields of winter rye or red clover grown in rotation. Barley and timothy yields were reduced by residues from an application of 1.0 and 0.5 kg ai/ha respectively in some years, but not in others. Studies in Alberta with picloram showed that application of this herbicide to soil in pots planted to potatoes gave severe injury to the crop at rates of application of 100 ppb and increased injury as the rate of application was increased (8).

POTATO TOP DESICCATION

Early studies on the desiccation of potatoes with chemical desiccants were conducted in Prince Edward Island in the late 1940's by Callbeck (1, 2, 3) who used various treatments of sodium arsenite or dinoseb. Work in Ontario on the cultivars Kennebec and Sebago showed that, after the crop has attained maximum yield, killing the vines 10 days earlier with chemical desiccant had no effect on tuber specific gravity as tubers continue to take up water (27).

Top desiccation of potatoes is mainly accomplished with the use of the herbicides diquat and dinoseb. Both products have problems associated with their use but little research has been conducted on the inter-relationships of the chemical and the plant to determine the factors that cause the erratic behaviour of the products from year to year. Studies at Charlottetown (28) showed that later application of diquat resulted in better desiccation on three cultivars and yield increase during the two week period after application was 2.3, 3.0, and 3.2 t/ha for Kennebec, Sebago and Bintje, respectively. Time of desiccant application also affected the proportion of small and large tubers in the yield. Application of diquat with a controlled droplet sprayer was shown to be not different from that with a conventional sprayer with both units giving a comparable level of top desiccation (22). In studies with Kennebec, top desiccation was shown to be better with a split application of diquat than with a single full dose (19) and the presence of excessive levels of nitrogen from applied fertilizer made desiccation more difficult. These data confirm other results with the Kennebec variety in a study in Quebec where nitrogen applied at 160 kg/ha made desiccation more difficult than when 80 kg/ha had been used (26). Differences in the ease of desiccation of different cultivars have been reported (9, 15) but no further studies have been carried out to define the reasons for these response differences. It is apparent that a profile of each cultivar is needed as to its ease of desiccation and recommendations must be cultivar-specific, not only for attainment of an adequate level of desiccation but also for maintaining high tuber quality needed for the end use of that crop.

CURRENT RESEARCH DIRECTIONS

Production of potatoes in Canada in 1985 was estimated to be at 117,282 ha, producing over 3 million tonnes and an average yield of 25.9 tonnes/ha for the country (Table 2). Major producing areas in eastern Canada are P.E.I., New Brunswick, Quebec and Ontario. These provinces produce approximately 76% of the potatoes grown in Canada with P.E.I. and New Brunswick producing approximately 50% of the national total. In western Canada, the major producers are Alberta and Manitoba.

Table 2. Area and production of potatoes in Canada and by province - 1985.

Area	Area Harvested	Total Yield	Yield/ ha
	ha	tonnes	tonnes
CANADA	117,282	3,039,177	25.9
Newfoundland	243	4,082	16.8
Prince Edward Island	29,705	799,062	26.9
Nova Scotia	1,700	36,197	21.3
New Brunswick	22,258	698,544	31.4
Quebec	19,385	460,008	23.7
Ontario	15,176	366,010	24.1
Manitoba	15,986	340,427	21.3
Saskatchewan	1,052	27,125	25.8
Alberta	8,094	208,656	25.8
British Columbia	3,683	99,066	26.9

Source - Statistics Canada Fruit and Vegetable Production. September 1986.

A telephone survey of researchers in University and government establishments that work on potatoes in Eastern Canada showed that only 1.11 person years professional are committed to weed research (Table 3). In Western Canada only 0.42 person years professional is committed to weed research (Table 4). The majority of this effort in both Eastern and Western Canada is used in testing of new products for weed control and top desiccation. Only a small amount of time is spent conducting research on development of data in those areas that are so necessary before in-depth systems can be researched and put into place in integrated weed control. There is, of course, some input by the chemical companies during the early life of new herbicide products but these studies tend to be solely of a developmental type and do not, as a rule, include comparison with competitors' products and are not always taken to yield.

Table 3. Person year input into potato weed control work in Eastern Canada - 1986.

Province	Worker	Person Year	Work Type
Ontario	Machado	.05	testing, microtubers
	O'Sullivan	.01	cultivar tolerance
	Shaw	.05	testing
Quebec	Leroux	.20	testing
	Rioux	.20	testing, top kill
New Brunswick	-	0	
Nova Scotia	-	0	
Newfoundland	-	0	
Prince Edward Island	Ivany	.60	testing, top kill competition
Total		1.11	

Table 4. Person year input into potato weed research studies in Western Canada - 1986.

Province	Worker	Person Year	Work Type
British Columbia	Freeman	.05	testing cultivar tolerance
Alberta	Moyer	.05	testing
	Esau	.12	testing cultivar tolerance
Saskatchewan	Dabbs	.10	testing
Manitoba	Friesen & Wall	.10	testing cultivar tolerance
Total		.42	

An analysis of the abstracts printed in the Research Report of the Expert Committee on Weeds for the Eastern Section for the 10 year period 1977-86 confirms the above data as there are approximately 315 abstracts during this period and 89% deal with testing for control of annual weeds, quackgrass, and potato top desiccation (Table 5). The remaining 35 abstracts deal with areas of basic studies but, for the most part, are studies on the differential tolerance of potatoes to herbicides and interference effects of quackgrass on growth and yield. In Western Canada, a total of 184 abstracts were published during this period and 91% deal with testing (Table 6). With the development of the newer post-emergence herbicides for the control of quackgrass, there has been an increase in abstracts in Eastern Canada on control of this weed but, unfortunately, there has been a marked decrease in research on potato top desiccation. There have been 10 workers submitting abstracts in the past few years in the East and 7 in the West and half of these are in universities or government laboratories and the remainder are in industry.

Table 5. Subject area of abstracts on potatoes in Expert Committee on Weeds - Eastern Canada Section Research Report from 1977 to 1986.

Year	Number of Abstracts	Number of Workers	Type of Abstract			
			Annual Control	Quack Control	Basic Studies	Top Kill
1977	18	6	7	3	3	5
1978	35	9	17	2	5	11
1979	31	7	14	2	4	11
1980	34	9	18	4	5	7
1981	43	13	17	9	5	12
1982	30	9	16	4	3	7
1983	34	9	16	6	4	8
1984	23	10	13	8	0	2
1985	33	10	8	18	4	3
1986	34	10	16	14	2	2
Totals	315	-	142	70	35	68

Table 6. Subject area of abstracts on potatoes in Expert Committee on Weeds - Western Canada Section Research Report from 1977 to 1986.

Year	Number of Abstracts	Number Workers	Type of Abstract			
			Annual Control	Quack Control	Basic Studies	Top Kill
1977	15	5	13	-	2	-
1978	18	3	16	1	1	-
1979	16	5	14	-	1	1
1980	25	10	21	1	2	1
1981	20	9	18	1	-	1
1982	18	8	17	-	1	-
1983	21	9	20	-	1	-
1984	19	6	16	-	3	-
1985	19	6	16	-	3	-
1986	13	5	11	-	2	-
Totals	184	-	162	3	16	3

FUTURE DIRECTIONS

Research in weed science in the potato crop will not advance rapidly in the future with the present manpower situation. The evaluation of herbicides and herbicide mixtures at various locations over several seasons for the control of annual and perennial weeds and the development of use patterns for crops are important objectives, as simple screening tests are no longer adequate to provide the information necessary for safe, effective recommendations to be given to farmers. Each researcher must have as a component of his program a testing function so as to be aware, at an early date, of the newest materials being developed by industry. Entrance late in the scheme of development puts a researcher behind in relation to growers and causes frustration for both as important data are not available. There is also the problem of the newer herbicides being more specific for crop and weeds controlled and the different responses in different climatic areas of the country which means work has to be done across the country and cannot be concentrated at one or two locations.

Research is also needed on the biology of perennial broadleaf weeds that are problems in potato crops but this cannot be done with current levels of support. More research is also needed on weed interference in the potato crop so as to establish the threshold levels of individual weed species, as well as various types of weed mixtures, before it can be determined if the herbicide can be eliminated from a field and the most effective use of available herbicides can be made.

The weed scientist is aware of an important part to be played in the future of pest management. It was realized some time ago that a more balanced approach between chemical, mechanical, cultural and biological control methods for weeds in our agroecosystems was required. Research priorities developed at the June, 1977 work planning meeting on weeds listed three top priority activities that are part and parcel of an integrated weed management system.

They are as follows:

1. The assessment of crop losses caused by weeds, including the development of survey methodology and weed competition research, leading to the development of models for predicting returns from weed control, when applied to specific grower situations.
2. Research on the interaction of herbicides when used in mixtures and the interactions of herbicides with other pesticides, non-target organisms such as insects, diseases, etc. and fertilizers.
3. Research on the development of integrated weed management systems.

It was pointed out in 1977, that the key for the future is collaboration, particularly as it applies to interdisciplinary research with all disciplines engaged in deriving the recipe for a production package on a crop (29). However, it was forecasted that the weed science contribution to the development of a total pest management system would be limited unless additional manpower was made available. This prediction has become fact, in the case of potatoes, as little has been done on weed management systems for the crop and the few researchers involved have opted for the development of safe, effective herbicides to solve the problems of weed control facing the farmer. It is suggested that, with the pressures of problem solving now being most important, one cannot be surprised at this direction in research. There is relatively poor support for weed research compared to the support given entomology and plant pathology, even though the losses in yield and quality caused by weeds exceed the losses attributed to other crop pests. Lack of support for more basic studies has also forced researchers to move in this direction so as to get the immediate fix and studies on interference, weed biology, and a number of more detailed studies have had to be delayed or conducted in piecemeal fashion as time and resources allowed. This must change if necessary work is to be completed. A truely national program of potato research dealing with all of the aspects that are necessary in an integrated program must be put into place.

The following is a list of research priorities in decreasing order of importance as determined by the authors. However, many could be considered of equal importance. All have been proposed before. Again, to implement such a program will require increased resources.

1. The ECW Action Plan on Crop Losses Caused by Weeds remains as a top priority research need. It is estimated that 22.1 PY professional and 31.0 PY support will be required to develop crop loss and integrated weed management systems in the Research Branch.

2. There is a need to consider the interrelationships of herbicides and their effects on plant growth when used as soil or as foliage treatments along with insecticides, fungicides, nematicides and other pesticides and fertilizers. A better understanding of the multiple use of pesticides on crop growth and soils would insure safe use. This is a complex problem requiring close cooperation of scientists in the various phases of crop protection.

3. Information is needed on the interacting influences of mixtures of herbicides on the movement and efficiency of the herbicide mixture. The use of mixtures and various combinations of herbicides and methods of application to allow for alternate chemicals helps to reduce the chance of soil and crop residues and helps to discourage the build-up of tolerant weed species.

4. Research on the development of integrated weed management systems is needed to optimize use of chemical, mechanical, cultural or biological control.

5. Cultivar effects of various herbicides are taking on more importance and future tests must consider these effects to a greater degree. The adequate evaluation of the herbicide tolerance of newly licensed varieties must be provided through increased collaboration of weed scientists, plant breeders and the herbicide industry.

6. The growth characteristics of potato cultivars must be elucidated to determine how these affect top desiccation and to permit development of recommendations for top desiccation on a cultivar-specific basis.

7. More work is needed on life cycles and biology of weeds and on biological and cultural control of weeds.

8. Research should be intensified to determine the means of reducing the development of weed species resistant to herbicides.

9. Crop rotations may be restricted by herbicidal residues. As new herbicides are developed, information is required to determine herbicide residues in the soil that can cause injury to certain crops.

10. Chemical methods of killing weed seeds in the soil are critically needed. Chemicals might be used to break dormancy of weed seeds or stimulate them to germinate when no crops are growing and thus reduce potential herbicide problems in both soils and plants.

11. More consideration should be given to effects on the total environment when using herbicides and other pesticides. Substantial research attention is needed to gain a better understanding of the selective toxicity of herbicides and other pesticides, including their fate in plants, soils and water and their possible side effects on non-target organisms.

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ROLE OF WEEDS IN POTATO VIRUS SPREAD

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ABSTRACT

Although no potato virus-infected weed hosts have been described in Canada, the genera containing virus reservoirs in other countries do contain several species in Canada. For a complete understanding of the mosaic disease of potato in eastern Canada, a survey of weed hosts is needed. The survey should be performed to include large areas in the potato-growing region, should use the most sensitive detection method available, and should be performed at different times during the growing season.

RÉSUMÉ

Bien qu' aucune mauvaise herbe n' ait été décrite comme réservoir de virus de la pomme de terre au Canada, les genres de plantes servant de réservoirs dans d' autres pays sont représentés par plusieures espèces Canadiennes. Pour bien comprendre l'épidémiologie de la mosaïque de la pomme de terre dans l'Est du Canada, un inventaire des mauvaises herbes pouvant servir de réservoirs à virus se doit d'être faite. Cet inventaire se devrait d' inclure des zones importantes de la région productrice de pomme de terre, devrait utiliser les techniques de détection les plus précises, et devrait se faire à plusieurs intervalles pendant la saison de croissance.

INTRODUCTION

At first glance, the subject assigned to me appeared straightforward and should have included the role of weed hosts for potato diseases caused by bacteria, fungi, viruses and viroids. However, because little work has been done on this aspect in Canada, and because most of the literature is from the U.S.S.R. and other countries where weed species may be entirely different, the scope of the present paper has been curtailed to include only potato viruses prevalent in Canada. (See Hiruki, these proceedings, for weeds and mycoplasma diseases). It is the aim of this paper to present a case for more emphasis on the investigation of the role of weeds in areas where a particular disease has been prevalent and whose epidemiology is not fully understood.

THE STATUS OF WEEDS IN VIRUS DISEASE PERPETUATION

It has been pointed out that most of the world's population is fed by 12 plant species (three cereals, rice, wheat, and corn; two sugar plants, beet and cane; three root crops, potato, sweet potato, and cassava; two legumes, bean and soybean; and two tree crops, coconut and banana). About 15% of 630 viruses or virus-like conditions reported have been described from these plant species (16). The number of angiosperm species is commonly reported to be about 250,000 (24), thus, about 15% of the viruses or virus-like conditions have been described from about 0.005% of the known species. Therefore, a large number of viruses await their discovery. Work has shown that weeds and wild plants are commonly infected with viruses. For example, an investigation of wild plants in the Royal Botanical Gardens at Hamilton, Ontario, showed that of the 29 plant species sampled at different periods of growth, virus infection was observed in each species at one or more stages of growth. The per cent infection varied from 1.4 to as high as 66.6% (15). Similarly, 44 plant species were surveyed for infection with tomato spotted wilt virus in Hawaii and all were found infected with the virus in one or more locations in Hawaii (6). This is particularly important when weeds also serve as a reservoir of vectors of viruses. Thus, the role of PVY-infected seed potatoes was implied when potato growing was started in new areas of Florida where PVY infection of pepper and tomatoes increased dramatically. Potato virus Y (PVY) was assumed to spread from potato to weeds, especially Solanum gracile Otto and S. nigrum L., which also are hosts for various species of aphids. From the weeds, PVY spread to pepper and tomato crops causing considerable losses in some areas. But no PVY infection in these crops was found in other areas where potato cultivation was not introduced, although weeds and vectors were present in both areas (21).

The identification of weed carriers of viruses can aid in the understanding of the ecological relationships that cause disease outbreaks. For example, potato tubers, when artificially inoculated with tobacco rattle virus (TRV), are susceptible only during a short period of time when they have grown to a considerable size. In such situations, late season weeds, especially Solanum sarrachoides and Amaranthus retroflexus, may play an important role in TRV epidemiology by providing a readily available source of inoculum. They may even account for perpetuation of the inoculum in the long term (13). An outbreak of alfalfa mosaic virus in the Origanum (Origanum vulgare L.) crops was associated with the occurrence of the same virus in Cavanilles Caro (Pitraea cuneato-ovata), a perennial weed plant which may carry the virus over winter (10).

WEEDS AND POTATO VIRUSES

In Canada, more than a thousand different plants can be designated as weeds. However, only about 230 species are considered important economically (11). No reports exist linking potato virus disease spread and weed hosts in Canada. This situation is analyzed below.

Table I lists various plant species which have been reported as virus reservoirs from other countries. Potato viruses S, X, Y and tobacco rattle virus have been recovered from 10, 21, 25 and 18 plant species, respectively. Potato viruses S and Y, which have narrow experimental host-ranges, have been found in as many weed hosts as the potato virus X and tobacco rattle virus, which have wide experimental host-ranges. Although several plant species belonging to these genera from which potato viruses S, X, Y and TRV have been recovered (Table I) are also present in Canada (Table II), no report exists linking potato viruses and a weed host in Canada. The mosaic disease of potato has been prevalent in Canada, and particularly in New Brunswick (see other presentations, these proceedings), since the 1920s; therefore, the possibility of some of these weeds serving as hosts for PVY is most likely.

Although it has been stated that there are no known overwintering hosts for PVY in the northeastern seed-growing areas of Canada and U.S.A., including New Brunswick (3), it appears that no surveys for weed hosts have been reported. There may have been small-scale weed surveys with no PVY hosts being found. However, it must be pointed out that weed reservoirs may be undetectable unless extensive surveys are made. For example, when more than 9,000 plant samples were collected and analyzed for tomato spotted wilt virus, 44 plant species, representing 16 families, were found infected with the virus. Twenty-five species were considered important reservoirs of the virus. From these, 24 new hosts for the virus were identified (6). A few reports of a weed host for viruses have been made from western and eastern Canada (4,22,23). These were studied mainly because they developed virus-like symptoms. However, most virus reservoirs may be symptomless carriers of viruses and can be detected only by an extensive survey of plant species in a region at various stages of growth.

TABLE I

PLANT SPECIES REPORTED AS NATURAL HOSTS FOR POTATO VIRUSES S, X, Y, AND TOBACCO RATTLE VIRUS FROM VARIOUS COUNTRIES

Scientific name	Common name	Potato viruses S	X	Y	TRV	Country
Agropyron repens Beauv.	Couch grass	-	-	$+^{1}$	-	U.S.S.R.
Amaranthus retroflexus L.	Redroot Pigweed	$+^{1a}$	$+^{1,13}$	+1	+13	U.S.A., U.S.S.R.
Anchusa arvensis M. Bieb.		-	-	-	$+^{7}$	Scotland
Anchusa officinalis L.		$+^{1}$	$+^{1}$	$+^{1}$	-	U.S.S.R.
Artemisia douglasiana Bess	Sage brush	-	+	-	-	U.S.A.
Barbarea arcuata Reichb.		$+^{1}$	$+^{1}$	$+^{1}$	-	U.S.S.R.
Bidens frondoso L.	Beggarticks	-	$+^{2}$	-	$+^{2}$	U.S.A.
Brassica geniculata Desf.		-	-	+	-	U.S.A.
Capsella bursa-pastoris (L.) Medic.	Shepherd's purse	$+^{1}$	$+^{1}$	$+^{1}$	-	U.S.S.R.
Ceratoides lanata	Winterfat	-	$+^{2}$	-	$+^{2}$	U.S.A.
Chenopodium album L.	Lamb's quarters	-	$+^{2}$	$+^{18}$	$+^{2,7}$	Argentina, Scotland, U.S.A.
Datura ferox L.		-	-	$+^{9}$	-	Argentina
Datura metel L.		-	-	$+^{19}$	-	India
Datura meteloides A.DC.	Jimson weed	-	-	+	-	U.S.A.
Euphorbia falcata L.		$+^{1}$	$+^{1}$	$+^{1}$	-	U.S.S.R.
Erodium cicutarium L'Her	Filaree	-	-	-	$+^{8}$	U.S.A.
Helianthus annus L.	Sunflower	-	$+^{2}$	-	$+^{2}$	U.S.A.
Heterotheca grandiflora Nutt	Telegraph weed	-	+	+	-	U.S.A.
Hieracium sp.		-	-	-	$+^{7}$	Scotland
Matricaria sp.		-	-	-	$+^{7}$	Scotland
Nicotiana glauca Graham		-	$+^{2}$	$+^{2}$	-	U.S.A.
Physalis angulata L.		-	-	$+^{12}$	-	U.S.A.
Physalis mendocina Phil		-	-	$+^{9}$	-	Argentina
Physalis virginiana Mill		-	-	$+^{12}$	-	U.S.A.
Physalis viscosa L.		-	-	$+^{18}$	-	Argentina
Plantago lanceolata L.	Narrow leaf plantain	$+^{1}$	$+^{1,2}$	$+^{1}$	-	U.S.A., U.S.S.R.
Plantago major L.	Broad leaf plantain	$+^{1}$	$+^{1,2}$	$+^{1}$	$+^{2}$	U.S.A., U.S.S.R.
Polygonum aviculare L.	Prostrate knotweed	-	-	-	$+^{7}$	Scotland
Polygonum convolvulus L.	Wild buckwheat	-	-	-	$+^{7}$	Scotland, U.S.A.
Portulaca oleracea L.	Purselane	-	-	-	$+^{2}$	U.S.A.
Rumex confertus Willd.		$+^{1}$	$+^{1}$	$+^{1}$	-	U.S.S.R.
Salix sp.	Willow	-	$+^{2}$	-	-	U.S.A.
Senecio vulgaris L.		-	-	-	$+^{7}$	Scotland
Setarea viridis	Green foxtail	-	-	-	+	U.S.A.
Solanum atriplicifolium		-	-	$+^{18}$	-	Argentina
Solanum atropurpureum Schrank		-	-	$+^{5}$	-	Brazil
Solanum chacoense Bitt.		$+^{20}$	$+^{20}$	-	-	India

TABLE I - (Continued)

Scientific name	Common name	Potato viruses				Country
		S	X	Y	TRV	
Solanum nigrum L.	Black nightshade	-	-	+[14]	-	India, U.S.S.R.
Solanum sarrachoides Sendt.	Hairy nightshade	-	+[2]	-	+[2]	U.S.A.
Sonchus arvensis L.		+[1]	+[1]	+[1]	-	U.S.S.R.
Stellaria media Vill.		-	-	-	+[7]	Scotland
Tribulus terrestris L.	Puncture vine	-	+[2]	-	-	U.S.A.
Viola arvensis Murr.	Wild pansy	-	-	-	+[7]	Scotland
Viola tricolor L.	Pansy	-	-	+[17]	-	India
Xanthium strumarium L.	Broadleaved cocklebur	-	+2	-	+2	U.S.A.

[a] Numbers refer to Literature Cited.

TABLE II

PLANT SPECIES FOUND IN CANADA, RELATED TO GENERA IN WHICH POTATO VIRUS S, X, Y AND TRV HOSTS HAVE BEEN REPORTED IN OTHER COUNTRIES

		Species in Canada[a]
Agropyron	Gramineae	3
Amaranthus	Amaranthaceae	4
Anchusa	Boraginaceae	0
Artemisia	Compositae	2
Barbarea	Cruciferae	2
Bidens	Compositae	1
Brassica	Cruciferae	5
Capsella	Cruciferae	1
Chenopodium	Chenopodiaceae	6
Datura	Solanaceae	1
Euphorbia	Euphorbiaceae	7
Helianthus	Compositae	0
Hieracium	Compositae	4
Matricaria	Compositae	2
Nicotiana	Solanaceae	0
Physalis	Solanaceae	3
Plantago	Plantaginaceae	5
Polygonum	Polygonaceae	10
Portulaca	Portulacaceae	1
Rumex	Polygonaceae	7
Salix	Salicaceae	0
Senecio	Compositae	4
Setarea	Gramineae	3
Solanum	Solanaceae	4
Sonchus	Compositae	2
Stellaria	Caryophyllaceae	2
Viola	Violaceae	3
Xanthium	Compositae	1

[a] Species in Canada were based on the basis of citation (11).

The method of virus detection can play an important role in extending the host-range of a virus. For example, detection of TRV and PVX by assay hosts, immunodiffusion serology and leaf dip electron microscopy identified only three species infected with TRV and two with PVX (8,13). In contrast, ELISA (enzyme-linked immunosorbent assay) detected 12 species infected with TRV and 11 with PVX (2).

Identification of weeds as hosts for potato viruses may depend on the locations where the weeds were surveyed. For example, in Allen and Davis' study, weeds within the field planted with PVX-free seed potatoes did not contain PVX, whereas in fields planted with PVX-infected potatoes, PVX was found within weeds (2).

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EVALUATION OF LOSSES IN POTATOES

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ABSTRACT

This brief review shows that losses in yield in potatoes caused by insects, weeds, diseases and nematodes are difficult to estimate accurately because of the complexity of the interaction of plant growth development and the time and severity of pest infestation. However difficult the process, the need for accurate estimates is extremely important as growers need to be able to make accurate economic assessments of the need for pesticides.

RESUME

Cette revue concise démontre qu'il est difficile de déterminer les raisons précises pour une perte de rendement dans une récolte de pommes de terre, a cause de l'interaction complexe entre le degré de croissance chez la plante et le moment et le degré d'infestation causé par les parasites, soit insectes, mauvaises herbes, maladies ou nématodes. Toutefois, même si ce processus est difficile à établir, il est très important pour le producteur d'obtenir des données précises afin de prendre de bonnes décisions économiques vis à vis l'usage des pesticides.

INTRODUCTION

The potato, Solanum tuberosum L. is a very important vegetable crop with annual world production of 290 million tonnes. As a source of food for humans it ranks in fifth place after wheat, maize, rice, and barley (38). In Canada, yearly production is approximately 2.5 million tonnes; Ontario production is 380,000 tonnes, or 15.2% of this total (2).

On a world-wide basis, nearly 50% of potato production goes towards animal feed. The remainder is used for table stock, seed or manufactured products (e.g. starch). In Ontario, 50% of production is processed, about 7% planted as seed and the rest (43%) consumed as table stock (28).

With the introduction of chemical pesticides, potato production increased significantly from an average of 17 tons/acre to 21 tons/acre (38). However, while insecticides, fungicides, herbicides and nematocides have effectively reduced yield losses due to pests, they have also significantly increased the cost of production. Pests too, have adapted to the use of pesticides. For example, high levels of insecticide resistance in Colorado potato beetle (CPB), Leptinotarsa decemlineata (Say), (13,16, see Martel in these proceedings) and rapid development in potato late blight, Phytophthora infestans (Mont.) de Bary, of resistance to the effective systemic fungicide, metalaxyl (7) have brought on the spectre, once again, of increased losses due to pests. In addition, the recent history of low prices, caused, in part, by over production, has drastically influenced the economic viability of potato farmers.

These developments have led to the very active search for more cost efficient methods of production and to a re-thinking of pest control methods. Integrated Pest Management (IPM), the use and integration of different kinds of control (e.g. cultural, biological) with, if necessary, chemical application, is now favoured. A key consideration in determining the type of management is economics. The important questions are, what is the cost of the pest control procedure and is there a financial benefit in terms of increased or preserved yield?

Our work has attempted to answer these questions for some of the pests we have in Ontario. We would now like to present these results within the wider context of Canada and the rest of the world.

The body of literature on crop loss due to insects (41,50,51), weeds (1,4,24,48,50,51), pathogens (19,20,46,50), and nematodes (32) is quite extensive and the methods for establishing losses very elaborate (5,6,42). We use the term "crop loss" to describe that portion of yield lost in plots where the pest was present compared to the yield in plots where the pest was controlled, all other conditions being the same. Thus, potential yield for us was actual yield obtained in pest-free plots. Potential yield with different cultivars under different conditions of rainfall, irrigation, fertilization and pest pressure could be substantially different. However, if yield loss estimates were to be of value, then yields in control plots must correspond closely to those achieved by neighboring growers.

LOSSES DUE TO WEEDS

Although losses due to weeds are primarily due to competition for resources, especially water, high weed populations can also hinder harvesting. Potato cultivars vary in their ability to compete with weeds. Early emergence, rapid early growth and the ability to maintain a dense leaf canopy throughout the growing season are characteristics that enhance the ability of potatoes to compete with weeds (31, see Ivany and Freeman in these proceedings).

In a study of quack grass, Agropyron repens (L.) Beauv., competition with potatoes, it was found that delaying quack grass removal for 2, 4 or 6 weeks after crop emergence reduced total yield by 6%, 27% and 21%, respectively, with a concomitant loss of marketable yield (17). It has also been demonstrated that early competition causes greater losses than latter infestations. For example, yellow foxtail, Setaria glauca (L.)

TABLE 1
YIELD LOSSES IN POTATOES DUE TO INSECTS, WEEDS AND DISEASES

YEAR	SOURCE OF LOSS	PROGRAM APPLIED	YIELDS tonnes/ha	YIELDS $/ha*	LOSSES** %	LOSSES** $/ha
STRATHROY - mineral soil						
1981	-	IFH †	32.98	3440	-	-
1982	-		26.43	2973	-	-
Mean			29.71	3206		
1981	Insects	FH	16.39	1709	50.3‡	1731
1982			15.12	1701	42.8‡	1272
Mean			15.78	1705	46.6‡	1501
1981	Weeds	IF	26.34	2747	20.1‡	693
1982			22.47	2528	15.0	445
Mean			24.41	2637	17.6	569
1981	Diseases	IH	31.12	3246	5.6	194
1982			25.32	2849	4.2	124
Mean			28.22	3047	4.9	159
1981	Insects, Weeds, Diseases	O	12.51	1305	62.1‡	2135
1982			8.86	997	66.5‡	1976
Mean			10.69	1151	64.3	2055
THEDFORD MARSH - organic soil						
1982	-	IFH	14.25	1603	-	-
	Insects	FH	7.29	820	48.9‡	783
	Weeds	IF	4.18	470	70.7‡	1133
	Diseases	IH	6.83	768	52.1‡	835
	Insects, Weeds, Diseases	O	2.17	244	84.8‡	1359

* contracted price: $104.30/tonne (1981); $112.50/tonne (1982)

** loss relative to IFH program

† I-insecticide; F-fungicide; H-herbicide; O-none

‡ significant ($p<0.05$) loss relative to IFH program in same year

Beauv., and wild mustard, *Sinapis arvensis* L., emerging 1 week after potato emergence, caused a loss of 54% compared to a 16% loss when weed emergence was delayed until 3 weeks after potato emergence (31).

In our own study (47) we evaluated losses due to weeds on both mineral and organic soil. On mineral soil, Kennebec potatoes, with maximum crop protection, produced nearly 30 tonnes/ha; the commercial grower harvested nearly identical yields in adjacent fields, suggesting that conditions in our small plots were representative of the farm situation. The yield of Superior potatoes in organic soil was much lower at 14 tonnes/ha. Excessive rainfall during the growing season caused waterlogged soil conditions on several occasions and generally depressed yields.

Dominant annual weeds encountered on mineral soil were lamb's quarters, *Chenopodium album* L., redroot pigweed, *Amaranthus retroflexus* L., and barnyard grass, *Echinochloa crus-galli* (L.) Beauv. Low populations of the perennial weeds, field horsetail, *Equisetum arvense* L., and yellow nutsedge, *Cyperus esculentus* L., were also present. Although ground cover by weeds was only about 40% and was reached relatively late in the season, a significant 20% yield reduction in the absence of weed control was recorded in 1981 (Table 1).

Weed pressure was much higher in organic soils, reaching nearly 50% ground cover within 3 weeks of planting and virtually 100% by the sixth week. Dominant annual weeds were redroot pigweed, pursale, *Portulaca oleracea* L., and barnyard grass; a heavy flush of large crabgrass, *Digitaria sanguinalis* (L.) Scop., developed later in the season, causing severe problems at harvest, even in the herbicide treated plots. Failure to control the higher weed population in organic soil depressed yields by 70% (Table 1).

In the absence of a weed control program, yield losses ranged from a low of $445/ha on mineral soil to over $1100/ha on organic soil (Table 1). Chemical weed control costs ranged from $81/ha on mineral soil to $111 on organic soil (Table 2), proving a good investment, particularly on organic soil.

TABLE 2
COST* OF PESTICIDE PROGRAMS APPLIED TO POTATOES

YEAR	LOCATION	INSECTICIDE	FUNGICIDE	HERBICIDE	TOTAL**
1981	Strathroy	84.20	91.00	81.30	256.50
1982	Strathroy	98.50	105.40	151.10	355.00
1982	Thedford Marsh	197.70	188.50	111.40	497.60

* Cost of material + application; ** Costs in $/ha

LOSSES DUE TO PATHOGENS

The two major fungus diseases of potato are late blight and early blight, Alternaria solani (Ell. & Mart.), although there are many other diseases which can cause quite severe losses (20, see Platt in these proceedings). The trend in recent years for estimating losses has been to develop models relating disease assessment at various times during growth to yield at harvest (43,44,45) in the hope that some critical assessment point could be found upon which to base control recommendations.

A multiple point model developed for late blight (18) utilized a multiple regression equation with the increase in disease during 9 weekly periods as the independent variables and yield loss as the dependent variable. This equation allowed estimates of crop loss with an accuracy of 5%, nine times out of ten. An improved version allowing wider use was developed by MacKenzie and Petruzzo (27).

A single point model could not satisfactorily explain the percent yield loss (total tubers or US #1 tubers) caused by early blight. However, a multiple point model using disease severity assessments on day 56, 66, 76, 86 after sprout emergence for the cv. Norland and the same periods, plus disease severity on day 96 for the cv. Russet Burbank, explained over 70 percent of the variation in yields (44).

In our experiments (47) potato diseases were not a problem on the well drained mineral soil. A low infestation of early blight caused minimal loss (Table 1), barely warranting the cost of fungicide application (Table 2). The organic soils of the Thedford Marsh, situated in a low-lying area near Lake Huron, are frequently characterized by cool nights, high humidity and very heavy dews which are slow to dry in the morning. Although late blight did develop in these plots, the main disease was again early blight. Losses over 50% were recorded in fungicide-free plots (Table 1). A heavy fungicide program with a total of six sprays was applied; its benefits exceeded its costs by 4.4:1 (Table 2). For all three trials, our average loss of 20.6% exceeded the Canadian average of 13% reported by Cramer (8) but was biased by the very high disease loss occurring on organic soil. Our results are, however, less than those estimated for the U.S. (36). These authors suggest a 20% loss of total U.S. crop with fungicide application and an additional 20% loss if fungicides were not applied.

LOSSES DUE TO NEMATODES

It has been demonstrated for many years that nematodes cause significant losses in many vegetable crops, including potatoes (34, see Kimpinski and Olthof in these proceedings). It was shown in Ontario that Sebago and Superior potatoes treated with nematocides yielded about 40% more than the controls in 1978. In 1979, however, no significant yield increase was observed (23). Olthof et al. (33) showed that treated potato fields yielded 10-15 tonnes/ha more when soil fumigants were applied.

In spite of these demonstrated benefits, very few potato fields are treated for nematodes in Ontario (28) as a result of low value of potatoes compared with the high cost of soil fumigants. Granular aldicarb, applied for insect control, may provide some control of nematodes.

LOSSES DUE TO INSECTS

On a world-wide basis, aphids are considered the insect pests of greatest economic importance to potato production (38). Although their primary importance is as vectors of virus diseases, high populations can cause direct losses. In Canada, these pests are of concern primarily to seed potato producers. Most seed potatoes are grown in P.E.I. and New Brunswick (ca. 33,000 ha) although some 1,000 ha are also grown in Ontario and Quebec (S. Squire, OMAF, Alliston, Ont., personal communication). Relegation, as a result of aphid transmitted virus disease, of seed stock potatoes to much less valuable table stock is the major source of aphid caused loss in Canada (see Holliday and Parry in these proceedings). In the absence of control measures, direct losses caused by aphids were estimated at 14.5% in the U.S. (25).

Research on the CPB, over the past several years, has tended to concentrate on the relationship between defoliation and yield reduction (see Singh and Boiteau in these proceedings). It has been shown that mid-season defoliation has much more effect than early-, when the plants are able to refoliate, or late-, when tuberization is nearly complete (9, 10, 12, 15). Significant differences among cultivars must also be considered (9). A useful synthesis of data on defoliation, CPB populations and yield losses has been developed by Logan and Casagrande (26) in a series of equations relating CPB density at given degree-day accumulations to predicted yield losses. In the absence of control measures, average losses to CPB are 47±10% (40, 41).

The most destructive insect to potatoes in eastern North America is the potato leafhopper (PLH), Empoasca fabae (Harris) (28, see Thompson in these proceedings). Studies have shown a linear relationship between increasing numbers of PLH, and % hopperburn and decreasing yield (35, 39). The action threshold in Minnesota is 10 nymphs/105 leaves (3), while in Wisconsin, with a large acreage of alfalfa acting as a reservoir of adult PLH, the threshold is 25 adult PLH/25 sweeps when nymphal densities are 20/25 leaves and 100 adult PLH/25 sweeps when nymphal densities are $\leq$ 10/25 leaves (49). Yields in Wisconsin in unsprayed plots were, on average, ca. 40% lower than in those with the best levels of insecticide control (49).

In our own work, we found that in the absence of insect control significant losses of at least 42% were recorded in every trial (Table 1). Although CPB, potato flea beetle, PLH, tarnished plant bug and various aphids were all recorded in the plots, only PLH populations reached economic levels; PLH levels exceeded the threshold level established by Cancelado and Radcliffe (3) of ca. 1 nymph/10 leaves in all three trials. Potato vines collapsed because of hopperburn by 1 September in all trials. Although losses in these trials were over four times those reported in Cramer's (8) overview of insect losses in potatoes, they agree quite well with specific reports of PLH losses by Peterson and Granovski (35) and Schwartz and Klassen (40).

The cost of insect control was nearly twice as high in organic soil as in mineral soil (Table 2) - a reflection of the high cost of aldicarb and the need for a second application of fenvalerate. In every case, however, the benefits of insect control exceeded its cost by at least 3.9:1.

CONCLUSIONS

This brief review on crop loss evaluation has made it abundantly clear that the interaction between pest and crop is complex and fraught with the danger of oversimplification. Each researcher sets the parameters within which the work will take place, and while this leads to projects of manageable size, changes in cultivar and/or climate can lead to such different results that loss estimates often cannot be directly compared. There is also the problem of the interaction of pests competing for the same resource. The authors are aware of no studies considering joint effects of two pest groups (weed/insect, insect/disease, etc.), let alone the three or four that are often active.

The use of Economic Injury Levels, Action Threshold Levels, and Critical Assessment Points has certainly helped potato growers make dependable pest control decisions. The integration of economic considerations into the decision making process has also resulted in a more critical evaluation of research results. The need for education is still evident as Radcliffe (38) pointed out when referring to insect foliage damage, "...growers often have a lower threshold of tolerance than does the potato, which often results in unnecessary insecticidal treatment."

As research in IPM intensifies and potato crop development is juxtaposed with pest development and temporal appearance, the need for accurate, reliable economic thresholds assumes even greater importance. The cost of pesticides, the ecological considerations of their use and the development of pest resistance will continue to pressure researchers to develop alternate means of control to prolong the usefulness of chemical pesticides.

Recent research on pest management, grounded in the physiological and ecological growth characteristics of the potato (11,21,22,37) and heeding not only cost/benefit ratios (14,30,31) but also the growers concept of risk (29), holds a great deal of promise.

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EPILOGUE

Potato crop production is a major and essential component of the Canadian agricultural economy. It is also a complex production system that serves the tablestock, processing and seed industries. Pest protection is essential if the producers are to meet the requirements of each segment of the industry. Without pest protection some 62-85% of the crop yield would be lost to pests. The task of realizing pest protection is complicated by regional variations in the relative importance of these industries and of the pests. In British Columbia, major concerns are with the luteoviruses PLRV and BWYV and their aphid vectors whereas in Eastern Canada, it is the mosaic viruses. Here, the problem is made even more difficult by the existence of different complexes of viruses in the different provinces. In New Brunswick, Prince Edward Island and Quebec, the Colorado potato beetle is the most important phytophagous insect pest whereas in Ontario the potato leafhopper is as great a concern as the beetle and in British Columbia the beetle is of no concern.

In spite of these difficulties, the challenge of pest protection on potato has been met quite successfully. These proceedings provide many examples. The incidence of leafroll, mosaic, latent viruses S and X and other highly infectious pathogens like spindle tuber viroid has been reduced considerably throughout the years. As a result, growers can now count on relatively disease free seed tubers. Adequate chemical controls have been developed for insects, fungi, annual broadleaves and grasses as well as nematodes. Strict quarantine measures have been developed. The best example is probably the successful isolation of the golden nematode on the islands of Newfoundland and Vancouver.

Unfortunately, the bulk of our pest protection strategies depend on pesticides. The development of insecticide resistant pest populations demonstrates the risks of such a dependance, the need for prompt action. Many roadblocks have been identified. Our lack of knowledge on many biological and ecological aspects of the crop and its pests has been repeatedly mentioned as a major hinderance to progress. This lack of adequate knowledge is especially large for secondary pests but, it may surprise some, extend to primary pests like the Colorado potato beetle and the bacterial agent of ring rot. The prediction of inflights of aphid vectors is possible or being realized but the forecasting of the intensity of these flights cannot be achieved until basic research on the flight behaviour of aphids has been done. Modeling of the epidemiology of plant viruses is possible but requires additional data, especially in the field population dynamics of potato viruses. Semiochemicals offer promising control alternatives but their successful implementation is dependent on an increased understanding of the crop and the pests. Weed biology and the role of weeds in potato virus spread have also been almost entirely overlooked. Low budgets and reductions in research staff, especially for basic research, were generally thought to be at the source of this situation.

Many participants believed that a better protection of the potato crop could be achieved, even within the limitations of present techniques and knowledge, if an integrated effort from the different specialists existed. The first step in achieving it would be better and easier communication between the specialists.

A number of progress areas were outlined by each presentation. We think it might be useful to highlight a few:

*Chemical control: Application of pesticides accounts for some 40% of the cost of chemical control. Expansion of studies on new spray equipment achieving better spray deposition and better control would help prolong the useful life of pesticides, reduce application costs as well as environmental and health negative effects. Also, insecticide resistance management is becoming--and must be--an integral part of our IPM programs.

*Monitoring: A few pest monitoring and forecasting techniques are available (aphids, blight), a few economic thresholds (root lesion nematode) are available but most are under development. New, more sensitive and accurate pathogen detection technology and the modeling of pest and crop interactions will affect future monitoring programs throughout the country.

*Plant breeding: The breeding of varieties resistant to certain pests offers opportunities for major gains especially if done in integration with the other traditional areas of research in protection.

*Biorational control: Cultural methods such as crop rotation offer great potential. New strains of bacteria offer promising control of the Colorado potato beetle if hurdles of registration can be passed and sufficient research on the microbials and the beetle realized. Advances in biotechnology could have a large impact on the future of this B.t. and other microbial control agents.

*Inspection: Improved methods for the detection of pathogens in plants and/or vectors could make them routine enough to be incorporated in phytosanitary inspection networks.

These proceedings provide for the first time a review of our state of technology and understanding of the potato pests and their interactions with the crop. Overall, it is a success picture but when one looks more in-depth remedies found to many of the problems suffer from inadequacies. These inadequacies often result from the narrow biological base on which they had to be designed and from the single-discipline approach. IPM has been a key expression referred to for some time now. This review shows that it is necessary to implement it. It is feasible if potato specialists learn to plan their studies across disciplines and if decision makers provide a supportive and favorable environment.

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